
Assessing Targets for the Restoration of Herbaceous Vegetation in Ponderosa Pine Forests

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Abstract

A restoration project is considered a success when the initial target is met, but many targets are plausible. We evaluated the success of a restoration project in its 11th year since treatment in a southwestern ponderosa pine–bunchgrass community and the appropriateness of several targets. We measured the responses of (1) total standing crop; (2) standing crop of five functional groups (C₃ and C₄ graminoids, leguminous forbs, and nonleguminous perennial and annual forbs); (3) graminoid community composition; and (4) standing crop of five common graminoid species (*Festuca arizonica*, *Muhlenbergia montana*, *Elymus elymoides*, *Carex geophila*, and *Poa fendleriana*). Targets were quantified in remnant grass patches, which provided the standards for these targets, and were assessed in three other forest patch types (pre-settlement tree patches, post-settlement tree patches, and patches

where all post-settlement trees were removed). Patches where all post-settlement trees were removed reached target levels for total standing crop, C₃ and C₄ graminoid standing crop, graminoid community composition, and *M. montana*, *E. elymoides*, and *C. geophila* standing crops. Standing crop of legumes and of *F. arizonica* did not increase over time in any patch type. Targets were not met in pre-settlement patches or in patches where some post-settlement trees were left standing, suggesting that it is unrealistic to expect equal responses across all patch types. If increasing herbaceous standing crop is a major goal, practitioners should create gaps within the pine forest canopy.

Key words: biomass, C₃, C₄, legumes, *Elymus elymoides*, *Festuca arizonica*, herbaceous standing crop, *Muhlenbergia montana*, patch.

Introduction

The success of a restoration project can be quantified when targets are set prior to project initiation (Hobbs & Norton 1996; Bakker et al. 2000). Targets should be grounded in knowledge attained through previous research and ecological theory (Palmer et al. 1997), should be an accurate representation of the reference community (Aronson et al. 1995; White & Walker 1997), and must be realistic in order to be useful (Ehrenfeld 2000). Choosing the appropriate target can be difficult when little is known about long-term treatment effects. Therefore, defining appropriate targets can be an iterative process because knowledge of a system is attained through long-term monitoring or adaptive management (Holling 1978) and because specific restoration targets become accepted throughout the restoration community (e.g., Palmer et al. 2005).

Vegetation dynamics among forest patches within a restoration context is an underdeveloped area of community theory, and research in this area can benefit the natural

sciences and restoration practices (Palmer et al. 1997). Research on patch dynamics in both forest and grassland communities has elucidated mechanisms of regeneration through gap creation and turnover (White 1979; Pickett & White 1985; Aguilera & Lauenroth 1995; Busing & White 1997). Ponderosa pine forests have a distinct structure where clumps of pine trees are interspersed throughout a matrix of grassland vegetation. Therefore, vegetation in the ponderosa pine–bunchgrass ecosystem may exhibit aspects of both forest and grassland community dynamics. However, the rate of forest canopy turnover in semiarid pine forests (White 1985; Mast et al. 1999) is slower than in mesic temperate forests (Pickett & White 1985). Tree canopy closure in southwestern ponderosa pine old-growth stands ranges from 17 to 30% (Pearson 1923; White 1985), suggesting that open grass patches may have comprised greater than 70% of the pre-settlement landscape [but see Fulé et al. (2002) for a description of pre-settlement forests on the Kaibab Plateau]. We define “pre-settlement” as the era prior to 1876, which corresponds to Euro-American settlement of northern Arizona and the beginning of widespread fire exclusion (Mast et al. 1999). In contemporary ponderosa pine–bunchgrass communities, three main patch types occur: (1) pre-settlement (stands of trees that established before 1876); (2) post-settlement (stands of trees that established after 1876); and (3) remnant grass patches. In this study, we examined

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herbaceous standing crop within these patch types and within a fourth patch type, post-settlement removed, in which many of the post-settlement trees were thinned. These forest patch types were stable over the study period, though the interannual precipitation totals were highly variable (Fig. 1). Therefore, this study characterizes plant community structure within the dominant forest patch types over a range of interannual climatic conditions.

The primary goal of restoring southwestern ponderosa pine forests is to restore ecosystem health by altering forest structure to more closely resemble the range of variability evident in pre-settlement forests and by reintroducing ecosystem processes such as frequent, low-intensity surface fires (Covington et al. 1997; Moore et al. 1999). Inherent within the overall goal of this project were specific targets such as (1) restoring pre-settlement forest densities; size, age, and spatial distributions of trees (Fulé et al. 1997; Mast et al. 1999; Moore et al. 1999, 2004); and (2) increasing total understory herbaceous standing crop to pre-settlement levels. Assessing the success of meeting the first target (forest structure) utilizes hard evidence because thinning prescriptions are crafted according to site-specific extant structural evidence of pre-settlement forest conditions (Fulé et al. 1997; Mast et al. 1999). Forest structure can be assessed immediately after treatment. Prescriptions designed to emulate pre-settlement forest structure have been successful (Covington et al. 1997), though their utility depends on the presence of extant structural evidence (Moore et al. 2004), the availability of old-growth trees on the restoration site, and post-treatment mortality due to windthrow and scorch. Assessing the success of meeting the second target (herbaceous standing crop) requires a different approach, however, because direct evidence of pre-settlement herbaceous standing crop no longer exists. We used the range of herbaceous standing crop found within remnant grass patches on the restoration site as targets.

Remnant grass patches are a useful target because these areas yield “contemporary information from the site to be restored (same place, same time)” (White & Walker 1997:344). The reference sites are within the restoration site, and continued monitoring of these allows us to understand the range of temporal variability within the target. This strategy assumes that contemporary grass patches are representative of pre-settlement grass patches, but we felt this was reasonable because these patches have remained highly productive and diverse with virtually no non-native species present. This strategy also assumes that these remnant grass patches are not unique in some other way. In particular, why have they remained when all other areas are now occupied by trees? Kerns et al. (2003) found no difference in chemical and physical soil properties between remnant grass and post-settlement patches, suggesting that the post-settlement patches represent recent tree invasion of formerly grassy areas. Therefore, it is likely that the remnant grass patches have simply not been invaded by trees yet.

Changes in the understory cannot be determined immediately after treatment; monitoring over many years is required to determine vegetation responses. During 13 years of monitoring the herbaceous community at Gus Pearson Natural Area (GPNA), herbaceous standing crop increased significantly in treated areas relative to the control (Moore et al. 2006). Standing crop was calculated by weighting the standing crop of each patch type by the areal extent of the patch type and therefore did not examine standing crop dynamics within patch types.

In many projects and across many ecosystem types, practitioners have targeted total biomass (Bakker et al. 2000), abundances of functional groups (Palmer et al. 1997), and abundances of individual target species (Lambeck 1997; Goldstein 1999); the target depended on the questions asked. Therefore, we asked several questions about appropriate targets within this community: (1) Were we successful at meeting the original target of increasing total herbaceous standing crop to levels found within the remnant grass patches, and was the initial target realistic for all patch types? (2) Could functional group standing crop in remnant grass patches serve as a target? (3) Could graminoid composition in remnant grass patches serve as a target? (4) Could standing crop of individual graminoid species within remnant grass patches serve as targets? We address these questions by analyzing standing crop data that span 13 years (1992–2004) from a restoration site in northern Arizona.

Methods

Study Site

This study was conducted at the GPNA, located 10 km northwest of Flagstaff, Arizona, in the Fort Valley Experimental Forest, Coconino National Forest. The 4.3-ha study site ranges from 2,195 to –2,255 m in elevation and has a flat to gently rolling topography. Soils were derived from Tertiary basalt flows and cinders and are classified as a Brolliar stony clay loam and a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs (Kerns et al. 2003).

The average annual temperature is 7.5°C. Average annual precipitation is approximately 57 cm and follows a bimodal precipitation pattern, with approximately half of the precipitation occurring as rain in July and August and half as snow in the winter. Drought was common during this study, with 2002 being especially severe (Fig. 1). Weather data were taken from the Fort Valley Experimental Station weather records (USDA, Forest Service Rocky Mountain Research Station, Flagstaff, AZ) and from the Flagstaff Airport (NOAA 2005) when occasional data were missing from Fort Valley.

The study area was fenced to exclude domestic ungulates in 1950 (Olberding 2000). In 1992, a 2.4-m-tall fence was constructed to exclude wild and domestic ungulates from GPNA. GPNA was never harvested for timber

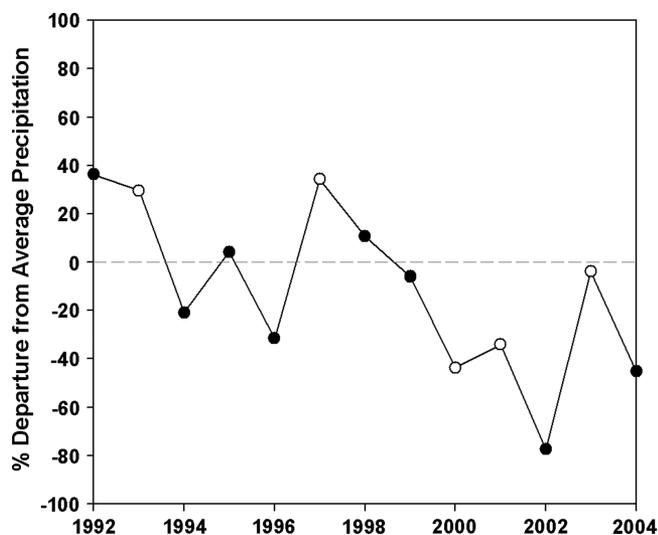


Figure 1. Annual precipitation during the study (1992–2004) as percent departure from the long-term (1953–2004) average. Annual totals include precipitation from the year before vegetation sampling (previous September through August). Filled symbols indicate years in which vegetation was sampled.

(Avery et al. 1976), and the last major fire in the area before this experiment occurred in 1876 (Dieterich 1980).

Ponderosa pine is the only overstory species on the study site. The understory is dominated by graminoid species, including Arizona fescue (*Festuca arizonica* Vasey), Bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey ssp. *elymoides*), Mountain muhly (*Muhlenbergia montana* (Nutt.) A. S. Hitchc.), Muttongrass (*Poa fendleriana* (Steud.) Vasey), and White Mountain sedge (*Carex geophila* Mackenzie). Dominant native forb species include American vetch (*Vicia americana* Muhl. Ex. Willd.), Flagstaff ragwort (*Senecio actinella* Greene), Pygmy bluet (*Houstonia wrightii* Gray), Rusby's milkvetch (*Astragalus rusbyi* Greene), Silvery lupine (*Lupinus argenteus* Pursh), Small-leaf pussytoes (*Antennaria parvifolia* Nutt.), Three-nerve goldenrod (*Solidago velutina* DC.), Western yarrow (*Achillea millefolium* L. var. *occidentalis* DC.), and Wheeler's thistle (*Cirsium wheeleri* (Gray) Petrak). The only shrub on the study site is Fendler's ceanothus (*Ceanothus fendleri* Gray).

Data Collection

In 1992, 10 circular plots with a diameter of 5 m were established within each of four patch types (pre-settlement, post-settlement retained, post-settlement removed, and remnant grass patches; Fig. 2) at GPNA, for a total of 40 plots. One plot per patch type was nested within a whole plot. Five whole plots were thinned, and five received a composite treatment (thinning, reduction of forest floor fuels, and prescribed burning) (see Covington et al. [1997] and Moore et al. [2006] for details of the experimental design). Pre-settlement patches (Fig. 2)

consisted of clumps of two or more large trees (mostly >30 cm) that established prior to 1876. Post-settlement retained patches (Fig. 2) consisted of a stand of small-diameter (<30 cm) trees that established after 1876. Post-settlement removed patches (Fig. 2) consisted of an area where all post-settlement trees were thinned and removed from the site, thereby creating an opening in the canopy. Remnant grass patches (Fig. 2) were located within open areas where no trees were present and where a representative sward of native grasses were present. Slope, aspect, and soil type were generally consistent across patch types, with the major difference being quantity and quality of canopy cover of overstory pine trees.

Patch types were not equally represented throughout the study area. Remnant grass patches occupied only 9% of the study area, leaving 91% dominated by trees. Prior to treatment, stands of post-settlement trees were the dominant patch type (70%). After treatment, the largest patch type in the study area was the post-settlement removed patch, which occupied 47% of the study area. Post-settlement retained and pre-settlement patches occupied roughly equal amounts of area, intermediate to the remnant grass and post-settlement retained patches.

Pretreatment data were collected in 1992. In 1993, thinning resulted in the removal of 2,226 trees/ha. All pre-settlement trees and trees greater than 40.6-cm diameter at breast height were retained. In addition, 5–15 smaller diameter trees were retained to replace stumps, snags, and downed logs and recreate the clumped pattern of the pre-settlement forest (White 1985; Edminster & Olsen 1996; Covington et al. 1997). Pine basal area was reduced by 45% in the post-settlement retained patches and by 95% in the post-settlement removed patches. The first prescribed burn was implemented in October 1994 (after data collection in that year), with subsequent burns in October 1998 and October 2002.

Herbaceous standing crop data were collected in 1992 (pre-treatment), 1994, 1995, 1996, 1998, 1999, 2002, and 2004. Field sampling occurred during a 2-week period in mid-September, which is the time of peak aboveground production and flowering for major understory species in northern Arizona (Clary 1975). We sampled two 1-m² (0.5 × 2.0 m) quadrats per plot. All live herbaceous vegetation rooted in the quadrats was clipped at ground level. Quadrats were arranged in a wagon-wheel configuration around the plot center, and clipping was rotated each year so that the same piece of land was not sampled 2 years in a row.

In 1992, standing crop was separated into graminoid and forb functional groups. From 1994 to 2004, herbaceous vegetation was separated into C₃ and C₄ graminoid, legume, nonleguminous perennial forb, and nonleguminous annual (including biennial) forb functional groups. Graminoids were further separated by species in 1994–2004. Samples were oven-dried at 70°C for 24–48 hr and weighed to the nearest 0.01 g. Data from the two quadrats per subplot were averaged together to yield a single value for each functional group or species on each subplot each year.



Figure 2. Example photos of each patch type used in this analysis: (A) pre-settlement, (B) post-settlement retained, (C) remnant grass, and (D) post-settlement removed. Plot centers are located between the three black buckets.

Data Analysis

Total standing crop data were analyzed by patch type for measurement years from 1994 to 2004. Functional group standing crop data were analyzed for measurement years from 1994 to 2004, as was standing crop of each of the five most abundant graminoid species (*F. arizonica*, *M. montana*, *E. elymoides*, *C. geophila*, and *P. fendleriana*). The other graminoid species were found on less than 25% of the plot-years, which made them unsuitable for individual analysis.

Herbaceous standing crop data did not meet assumptions of equal variance or normality so were $\ln(x + 1)$

transformed prior to all analyses. Transformations were mostly successful in stabilizing variances and in promoting normal distributions, though slight deviations remained for a few variables. Because analysis of variance (ANOVA) has been shown to be robust to slight deviations from assumptions, we used ANOVA in every case for simplicity rather than report nonparametric tests for the few variables that deviated slightly from the assumptions. All tests were conducted at $\alpha = 0.05$ using JMP-IN software (version 5.1.2; SAS 2004). Post-treatment standing crop data were analyzed using repeated measures multivariate

analysis of variance (MANOVA) with Greenhouse–Geisser adjustments to account for autocorrelation (Moser et al. 1990). We tested for burn, patch, and time main effects, patch \times burn interactions, and patch \times time interactions. Burn effects tested for difference between the thinning and composite treatments. Whole plots were included as a random blocking factor but were not of experimental interest and are not reported. Significant patch \times time interactions indicated that temporal dynamics differed among patches. Significant patch effects on total standing crop were followed by analyses comparing patches within each year. Significant patch effects on functional groups or individual species were followed by analyses comparing patches within the years 1994, 1999, and 2004 (endpoints and midpoint of the study period) to reduce the number of reported tests. These analyses were conducted using one-way ANOVA and Tukey's Honestly significant difference multiple comparisons tests. Because our objectives were not to determine the "best" treatment or combination of treatments for a particular result, we followed significant interaction effects with tests of single factors in order to determine in detail how patches differed within years. In general, the calculated F -statistics were much smaller for the interaction than for the main effects, suggesting that the main effects were more important.

Functional group proportions within pre-settlement, post-settlement retained, and post-settlement removed patch types were compared with the remnant grass patch in each year. Functional group proportions were analyzed with the likelihood ratio (G^2) contingency test (Ott & Longnecker 2001).

We conducted nonmetric multidimensional scaling (NMS) ordinations using PC-ORD software (version 4.25; McCune & Mefford 1999) to illustrate compositional differences in the graminoid community between patches over time (Clarke 1993). Separate ordinations were conducted for functional groups and for graminoid species. For each ordination, standing crop data were averaged across the 10 subplots per patch per year to yield a total of 28 data points (four patches within each of the 7 years). NMS arranges the plots in a configuration that minimizes the interplot distances (stress). We used the Bray–Curtis distance measure (Faith et al. 1987) 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 9,999 randomizations was used to determine how likely the observed stress value of the final solution would be by chance alone. Species that occurred on less than 5% of the plots were omitted from the ordination (McCune & Grace 2002).

Results

Total Standing Crop

Total herbaceous standing crop varied among patches and years (Table 1). Standing crop in the remnant grass

patches averaged 800 kg/ha in 1992, whereas standing crop in other patch types was less than 150 kg/ha (Fig. 3). Standing crop varied temporally in response to interannual climatic variability (Fig. 1) and spatially in response to patch type (Fig. 3). Beginning in 1995, standing crop in the post-settlement removed patches resembled that in remnant grass patches (Fig. 3). Standing crop in the post-settlement retained and pre-settlement patches remained less than that in the remnant grass patches (Fig. 3).

Functional Group Standing Crop

C_3 graminoid standing crop varied among patches and years, but the patch \times time interaction was not significant (Table 1). C_3 graminoid standing crop was similar between remnant grass and post-settlement removed patches and much lower in the post-settlement retained and pre-settlement patches (Fig. 4). C_4 graminoid standing crop varied among patches but not among years, but the patch \times time interaction was significant (Table 1). C_4 graminoid standing crop in the post-settlement removed patches increased to levels similar to that in remnant grass patches over time (Fig. 4); this result was driven primarily by increases in *Muhlenbergia montana* standing crop.

Legume standing crop varied among patches and years, and there was a significant patch \times time interaction (Table 1). Legume standing crop was greatest in the remnant grass patches in 1994 but did not differ from the other patches in 2002 and 2004 (Fig. 4). However, there was a significant burn effect on legume standing crop (Table 1), suggesting that fire caused an increase in legume production. Nonleguminous perennial forb standing crop varied among patches and years, but there was no patch \times time interaction (Table 1). Perennial forb standing crop was significantly lower in pre-settlement patches than in other patches (Fig. 4). Nonleguminous annual forb standing crop varied among patches and years, and there was a significant patch \times time interaction (Table 1). Annual forb standing crop did not differ among patches in 1994, was highest in the post-settlement removed and post-settlement retained patches in 1999, and was similar among post-settlement removed, post-settlement retained, and grass patches in 2004 (Fig. 4). There was also a significant whole-plot effect for annual standing crop ($p = 0.03$), suggesting that annual standing crop was spatially variable (whole-plot effects were not significant for other functional groups).

The NMS ordination (Fig. 5a) illustrates the strong initial differences in functional group composition among patches and how post-settlement removed patches became similar to remnant grass patches within two years of treatment. Relative proportions of functional groups in pre-settlement, post-settlement retained, and post-settlement removed patches differed from that in remnant grass patches most years. However, in 1995 the post-settlement retained patches were similar to the grass patches ($G^2 = 2.3$, $p = 0.686$), and in 2002 the post-settlement

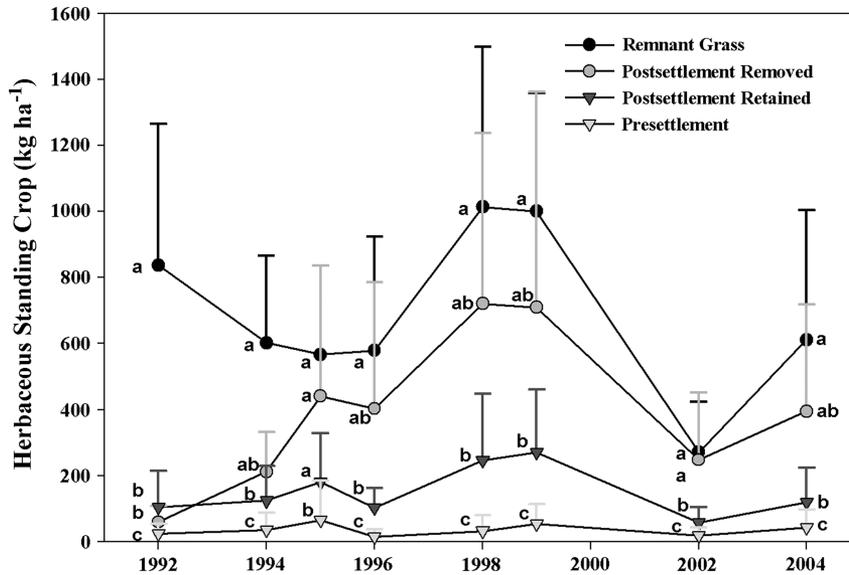


Figure 3. Total herbaceous standing crop (mean + SD) among patch types from 1992 to 2004. Pairwise comparisons of patches within years are reported for each year.

removed patches were similar to the grass patches ($G^2 = 5.5, p = 0.242$).

tion exhibited little change in the pre-settlement and post-settlement retained patches.

Graminoid Community

We identified 15 graminoid species across the study area. The analysis of graminoid community composition focused on the 11 species found on at least 5% of the plots. Graminoid community composition differed strongly among patch types initially (Fig. 5b), and the composition of post-settlement removed patches became more similar to that of the grass patches over time. Graminoid composi-

Individual Graminoid Species

Patch effects were significant for all graminoid species, but burn effects were not significant for any species (Table 1). *Festuca arizonica*, *M. montana*, and *Elymus elymoides* had significant patch × time interactions. For example, standing crop of *E. elymoides* was greatest in 1998 and 1999 in the post-settlement removed patches but did not change appreciably in other patch types. *Festuca*

Table 1. Summary of repeated measures MANOVA results for burn, patch, time, and patch × time interaction effects on total standing crop, standing crop of functional groups, and standing crop of individual graminoid species.

Standing Crop Variables and Associated Figure	Burn		Patch		Time		Patch × Time	
	F	p	F	p	F	p	F	p
Total								
Total standing crop	0.1	0.701	34.6	<0.001	13.2	<0.001	1.6	0.107
Functional groups								
C ₃ graminoids	0.7	0.419	29.6	<0.001	8.6	<0.001	1.7	0.090
C ₄ graminoids	1.2	0.297	14.3	<0.001	1.8	0.131	1.8	0.047
Legumes	5.4	0.049	24.7	<0.001	10.9	<0.001	3.0	0.001
Perennial forbs	0.1	0.751	6.5	0.002	14.4	<0.001	1.3	0.235
Annual forbs	4.6	0.065	7.9	0.001	14.1	<0.001	3.2	0.002
Graminoid species								
<i>Festuca arizonica</i>	0.2	0.693	19.4	<0.001	3.3	0.011	2.2	0.013
<i>Elymus elymoides</i>	0.04	0.839	21.3	<0.001	12.7	<0.001	2.9	0.001
<i>Muhlenbergia montana</i>	1.8	0.218	14.9	<0.001	1.5	0.217	2.0	0.031
<i>Carex geophila</i>	1.2	0.312	14.0	<0.001	2.1	0.082	0.9	0.520
<i>Poa fendleriana</i>	0.4	0.531	3.0	0.049	0.7	0.591	1.2	0.285

There were no significant patch × burn interactions, and the whole-plot (a random blocking factor) effect was only significant for annual forbs. Bold p values are significant ($p < 0.05$).

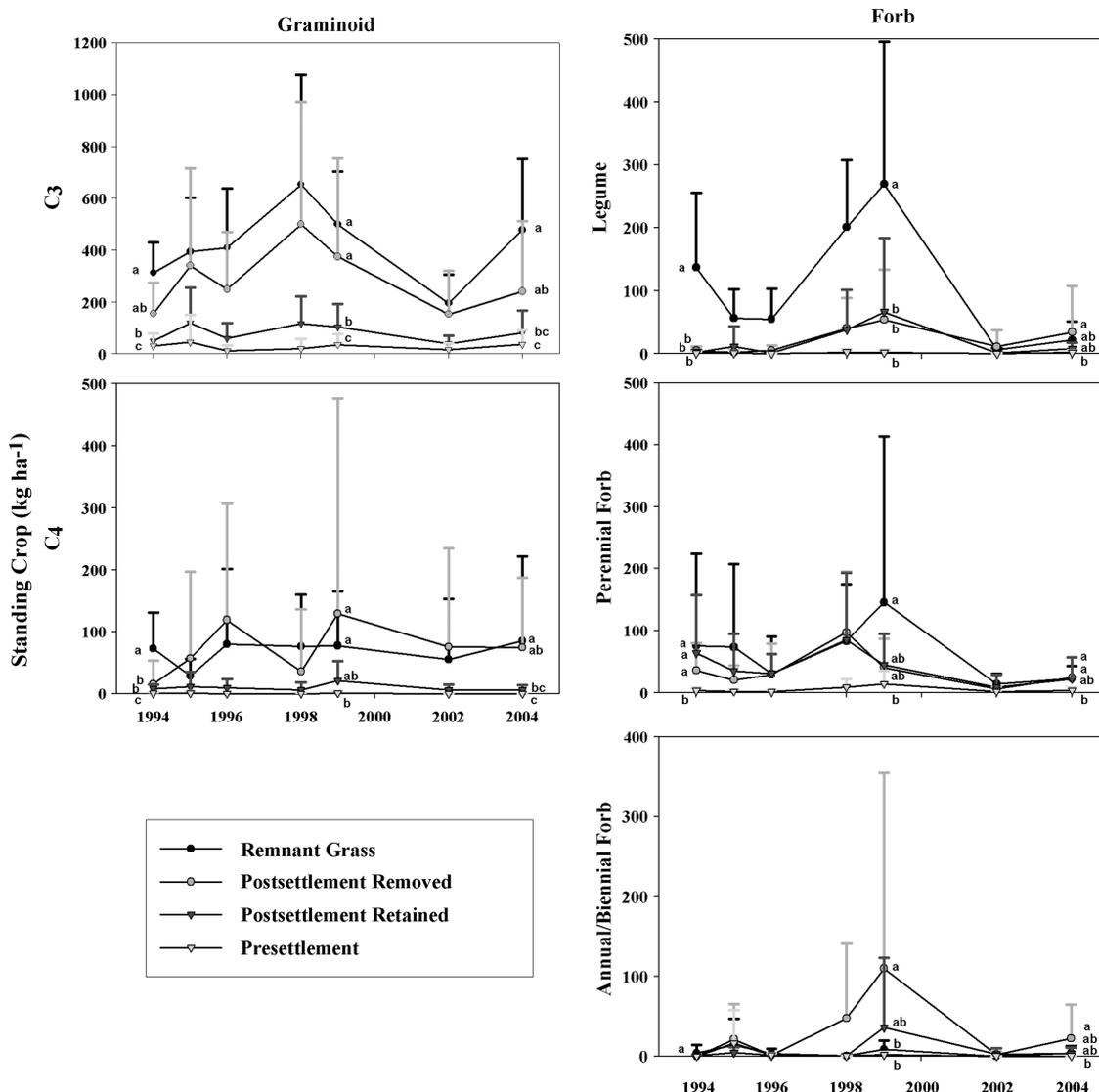


Figure 4. Standing crop (mean + SD) of functional groups among patch types from 1994 to 2004. Pairwise comparisons of patches within years are reported for 1994, 1999, and 2004. Note 3-fold difference in scale of y-axes.

arizonica was most abundant in remnant grass patches and did not increase appreciably in other patch types over time (Fig. 6). *Muhlenbergia montana* was most abundant in remnant grass patches in 1994; standing crop increased to similar levels in post-settlement removed patches but remained low in post-settlement retained and pre-settlement patches (Fig. 6). *Elymus elymoides* was abundant in remnant grass, post-settlement removed, and post-settlement retained patches in 1994. In 1999, it was most abundant in post-settlement removed and grass patches, but in 2004 it did not differ among patches (Fig. 6). *Carex geophila* was most abundant in remnant grass and post-settlement removed patches throughout the study (Fig. 6). *Poa fendleriana* did not differ in abundance among patches (Fig. 6).

Discussion

Was the Initial Target Met?

Remnant grass patches were chosen to represent the range of natural variability of herbaceous vegetation because they were highly productive, graminoid-dominated patches. The original restoration target for the ponderosa pine forest understory was to increase herbaceous standing crop to levels found in remnant grass patches. This target was met in the post-settlement removed patches within two years of treatment but was not met in the post-settlement retained or pre-settlement patches, suggesting that small trees (post-settlement retained) and large trees (pre-settlement) both negatively affected understory standing crop. Because the post-settlement removed patches occupied

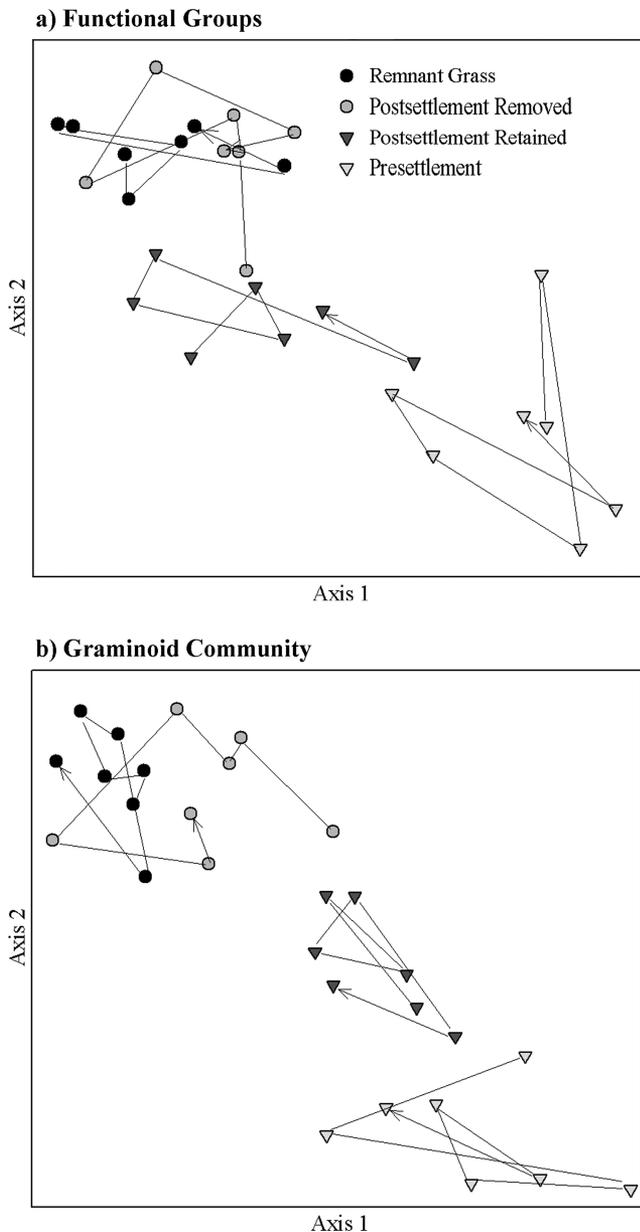


Figure 5. NMS ordinations of (a) functional groups and (b) graminoid composition among patch types from 1994 to 2004. Arrows connect data from subsequent measurement years for each patch type. The NMS of functional groups was determined using the standing crop of five functional groups on 28 plots; the final solution had two dimensions; stress = 6.2, $p = 0.0099$. The NMS of graminoid composition was determined using the standing crop of 11 species on 28 plots; the final solution had two dimensions; stress = 8.5, $p = 0.0099$.

47% of the study area, the overall result when patches were weighted by their areas was a significant increase in standing crop (Moore et al. 2006).

Was the Initial Target Realistic?

In retrospect, it was unrealistic to expect standing crop of the herbaceous understory to be equal among all patch

types 11 years after treatment. Pine trees intercept light and precipitation and compete with the understory vegetation for soil resources (McLaughlin 1978; Riegel et al. 1995). In addition, pre-settlement patches contain deep litter and duff layers (O_i + a + e horizons) that likely hinder tree and herbaceous seedling establishment (Sydes & Grime 1981; Facelli & Pickett 1991). Duff layers beneath large pines were likely present in pre-settlement times, but depths are deeper in contemporary forests after more than 100 years of litter accumulation (Sackett & Haase 1998). Cooper (1960) suggested that grasses grew up to the bases of large trees under a frequent fire regime, but there is little quantitative evidence to support this suggestion. Several studies have demonstrated negative overstory-understory relationships in contemporary ponderosa pine forests (Ffolliott 1983; Bojorquez Tapia et al. 1990; Moore & Deiter 1992; Bakker 2005). Based on the range of standing crops observed in this patch type, it is unreasonable to expect herbaceous standing crop to exceed more than 200 kg/ha within the pre-settlement patch type. Natural recruitment of herbaceous plants has not occurred beneath large pines in our study area during this 11-year post-treatment period, and we do not expect it to occur in the near future.

Because 45% of pine basal area was removed from the post-settlement retained patches, we expected a larger response than was observed in these patches. Apparently, the remaining trees intercept enough light and moisture to hinder a herbaceous response (Riegel et al. 1995), particularly during years of below-average precipitation. Open patches within the pine forest canopy are essential to stimulate recovery of the understory in southwestern ponderosa pine forests.

Interannual precipitation clearly plays a role in determining temporal dynamics of herbaceous standing crop in semiarid ponderosa pine forests (Fulé et al. 2002, 2005). The severe drought of 2002 is clearly evident in the reduction of standing crop across all patch types. We will address interannual climatic variation effects on the understory community more fully in future studies.

Can Functional Group Standing Crop Be a Target?

In a general sense, functional group standing crop can be used as a realistic target, although functional groups vary in response by patch type. In post-settlement removed patches, C₃ and C₄ graminoid standing crops increased to levels similar to those of remnant grass patches in a few years. In post-settlement retained and pre-settlement patches, C₃ and C₄ graminoid standing crops did not change appreciably.

The results for forb functional groups were not as consistent. Legume standing crop remained high in the remnant grass patches and did not increase appreciably within any other patch type. Nevertheless, legume standing crop increased in response to burning (Moore et al. 2006), which corresponds to results found in oak savannas in

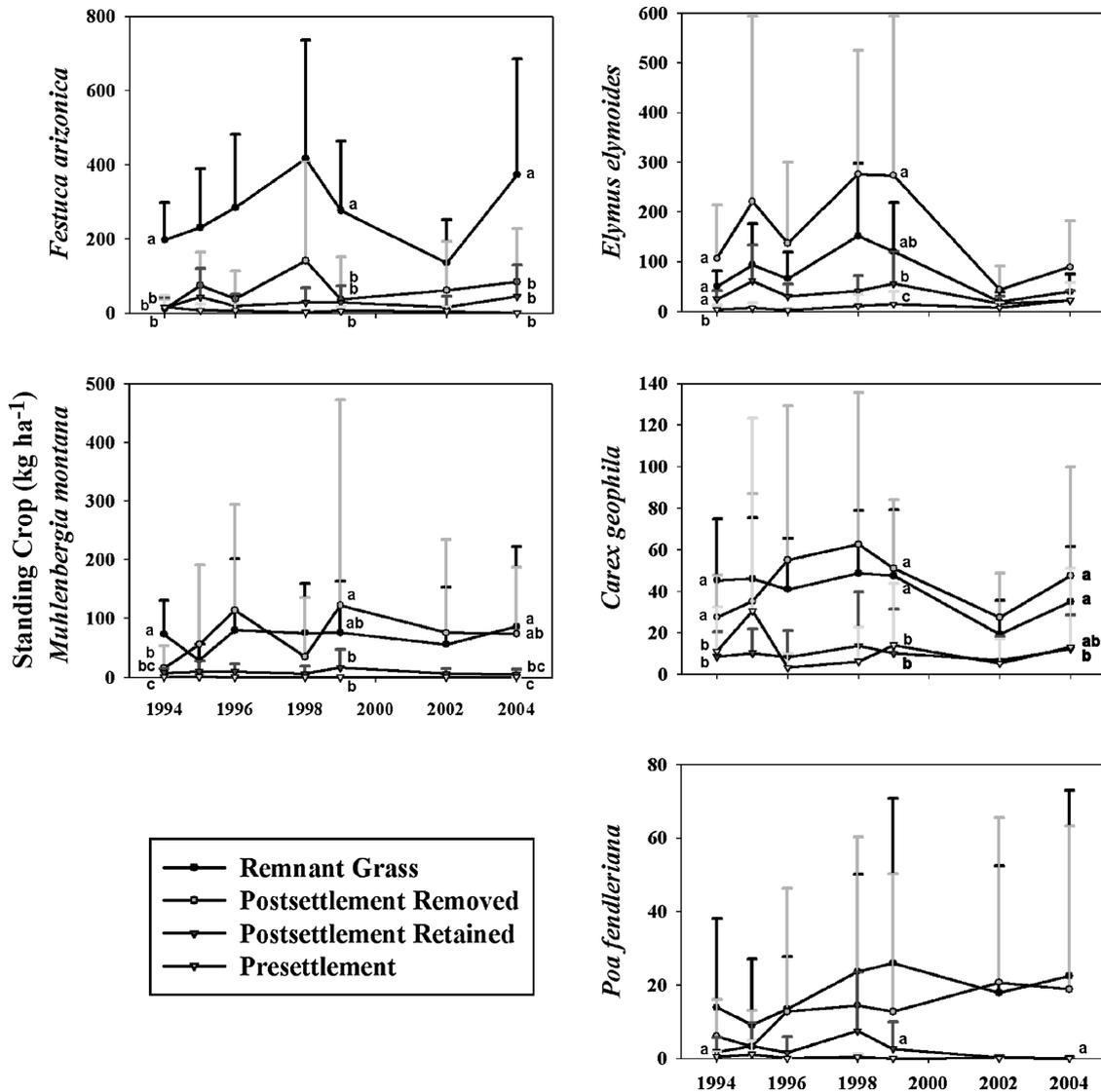


Figure 6. Standing crop (mean + SD) of dominant graminoid species among patch types from 1994 to 2004. Pairwise comparisons of patches within years are reported for 1994, 1999, and 2004. Note 10-fold difference in scale of y-axes.

Wisconsin (Leach & Givnish 1996) and subalpine forests in Wyoming (Schoennagel et al. 2004).

Perennial forb standing crop was similar among patches at the beginning of the study, which suggests that merely maintaining perennial standing crop levels is a sufficient goal, though future research should address possible compositional differences of perennial forbs between patches.

Interestingly, annual forb standing crop did not differ among patches initially but increased significantly in the post-settlement removed patches. We attribute this to the greater disturbance caused by tree thinning (and burning in the composite treatment) in these patches. Some of the annual (including biennial) standing crop was contributed by Common mullein (*Verbascum thapsus* L.), a non-native species. Native annual species may be important indicators of healthy ponderosa pine forests (Laughlin et al.

2004) but are generally small and contribute minimally to total standing crop. Therefore, a realistic goal for annual standing crop should be increasing richness of native annuals but not necessarily increasing standing crop of annuals because the productive annual species are often non-native.

Relative proportions of functional groups are an important aspect of the restoration target because we want to restore both productivity and community composition. For example, a highly productive patch dominated exclusively by a single species would not be an example of a successful restoration outcome because a diversity of functional groups is not represented. However, we do not recommend using relative proportions of functional group standing crop in the remnant grass patches as a restoration target unless increased productivity is achieved first. This can be understood by an example. Consider two patches

with similar proportions of functional group standing crop but vastly disparate total standing crop values. For instance, proportions of functional groups were similar in 1995 between post-settlement retained and remnant grass patches, but total standing crop was four times greater in the remnant grass patches. So, although the relative proportions of functional groups between the patches were the same, the two patches were not functionally equivalent because production levels differed so dramatically. Functional group composition could be used as a secondary target once the target for total standing crop has been achieved.

Can the Graminoid Community Be a Target?

Similar to total standing crop, the graminoid community can be used as a target, with recognition that pre-settlement and post-settlement retained patches will likely not meet expectations. Graminoid composition in post-settlement removed patches shifted toward compositional similarity with the remnant grass patches over time (Casey 2004).

Can Individual Graminoid Species Be Targets?

Individual graminoid species can be used as restoration targets, though many species are not common enough to be used as targets. Of the 15 graminoid species found on the study area, only five were abundant enough to be analyzed. Nevertheless, we expected interspecific differences in response because production of native species varies in response to forest structure and light levels (Naumburg & DeWald 1999; Naumburg et al. 2001).

Festuca arizonica had the greatest standing crop in the grass patches at the beginning of the study, so our goal was to increase its abundance in the other patches. We expected *F. arizonica* to increase particularly in the post-settlement removed patches because it performs well in high-light environments (Naumburg et al. 2001), but it did not increase in abundance in any patches. Dispersal limitation is a problem in many restoration projects (Verhagen et al. 2001; Donath et al. 2003), but we do not think *F. arizonica* was dispersal limited because seed is produced within the remnant grass patches every year. This suggests that specific requirements for seed germination or seedling establishment and survival of *F. arizonica* were not met within the other patch types. Germination for a similar species, *F. idahoensis*, has been reported to occur at 20/15°C and 23/4°C alternating temperature cycles (Baskin & Baskin 2001), which are similar to temperatures that occur during the growing season in northern Arizona. Though fescues tend to germinate readily in greenhouse conditions, it has been noted in the past that seeding fescue on rangelands was not very successful (Forsling et al. 1931) and that seeds of *F. idahoensis* and *F. ovina* are not highly germinable (Young et al. 1981). Alternatively, perhaps simply not enough time has lapsed since treatment for *F. arizonica* to establish itself, as it tends to be more common on undisturbed sites. Consideration of *F. arizonica* as a target species is warranted

because it is a very important and common C₃ bunchgrass in this system (Naumburg & DeWald 1999; Naumburg et al. 2001), though further research into establishment requirements for this grass would be necessary in order to meet desired goals.

Elymus elymoides is a generalist species that performs well in high light or dense shade conditions and is one of the few species that can tolerate dense forest conditions (Naumburg & DeWald 1999; Naumburg et al. 2001). *Elymus elymoides* standing crop was equally abundant in the remnant grass, post-settlement removed, and post-settlement retained patches at the beginning of the study, so our goal for this species was to maintain levels of this grass over time. *Elymus elymoides* standing crop tended to be larger in post-settlement removed than in remnant grass patches, suggesting that it filled a niche created by the thinning disturbance in the post-settlement removed patches. We expected a significant response to prescribed burns because this species appears well adapted to fire (Wright 1971; Young & Miller 1985; Vose & White 1991), but did not detect a significant burn effect. It appears that *E. elymoides* standing crop peaked 5–6 years after the experimental treatments began, though it is difficult to distinguish the reduced standing crop in 2002 and 2004 from drought effects. Because *E. elymoides* responds favorably to disturbance, it is an important species in this system and was likely an important grass in pre-settlement times when low-intensity fires occurred frequently.

Muhlenbergia montana was the only C₄ species included in these analyses and is generally associated with warm, sunny openings in the forest (Naumburg & DeWald 1999; Naumburg et al. 2001). In 1994, *M. montana* standing crop was most abundant in the remnant grass patches, so our goal was to increase *M. montana* standing crop in other patches over time. *Muhlenbergia montana* did increase in the post-settlement removed patches to levels similar to that in the remnant grass patches during the period of study as predicted based on its affinity with high-light environments, though its standing crop remained low in the post-settlement retained and pre-settlement patches. The pre-settlement and post-settlement retained patches apparently did not provide enough light for this C₄ species to become a dominant graminoid. This species is a very common grass in open areas in this system and would therefore serve as a good target species.

Carex geophila remained abundant in the remnant grass and post-settlement removed patches. Though we cannot say for sure that *C. geophila* was not abundant in the post-settlement removed patches prior to treatment, these data suggest that *C. geophila* could be a good target species because it responded rapidly to the removal of small-diameter trees.

Poa fendleriana standing crop did not differ among patches throughout the course of the study and therefore not a good candidate as a restoration target. However, both *Carex* and *Poa* species are cool-season C₃ graminoids that grow predominantly in spring and early summer, so

we may not have captured their maximum standing crops when we sampled in September. Future studies might address sampling date effects for early-season species.

Patch Size

Patch size will have a significant effect on the response of the understory vegetation. For instance, a small opening within a dense stand of pines will likely not provide the resources required for a productive understory. Remnant grass patches only accounted for 9% of the study area, though Covington et al. (1997) suggest that grass openings were larger and more frequent in pre-settlement times. Thus, prescriptions designed to emulate pre-settlement forest structure (Fulé et al. 1997; Mast et al. 1999; Moore et al. 2004) would therefore likely create openings that are large enough to permit positive responses by the herbaceous vegetation. We did not sample the patch types in proportion to each patch type's abundance because we used a balanced experimental design; therefore, we sampled remnant grass patches with greater intensity than other patch types. We do not think this biased our results because sampling error was actually smaller in the other patch types compared with the remnant grass patches. Pre-settlement patches averaged 0.055 ha in size (range 0.02–0.11 ha), within the range of old-growth group sizes reported previously (0.02–0.29 ha in White [1985]; 0.06–0.13 ha in Cooper [1960]). Patch size and shape are important elements of landscape-scale forest structure and should be addressed in future studies.

Conclusions

We conclude by commenting on the recommended list of key processes in restoration ecology that are needed for successful integration of restoration into land management (Hobbs & Norton 1996). We recognize that fire exclusion and other factors contributed to the irruption of pine densities in the early 1900s and have led to drastic ecosystem degradation in ponderosa pine–bunchgrass communities in northern Arizona (Covington & Moore 1994). Therefore, we have developed treatments that include the thinning of post-settlement trees to emulate pre-settlement forest structure (Mast et al. 1999) and the reintroduction of surface fires to reverse this degradation (Moore et al. 1999). Realistic goals for this system are the reduction of tree densities to levels found prior to Euro-American settlement and increased herbaceous productivity (Covington et al. 1997). Implementing restoration treatments over large scales can be costly but may be cost-effective compared with fire suppression costs (Snider et al. 2003). High costs are currently a major hindrance to landscape-scale forest restoration in the Southwest.

Easily observable measures of success include pine density and pine basal area and herbaceous standing crop or percent cover. Targets can be met on a landscape-scale through site-specific thinning prescriptions and use of pre-

scribed fire, and these restoration prescriptions have been incorporated into suggested management strategies for land-use agencies across the Southwest (Friederici 2003). Thinning treatments have reduced tree densities and thereby reduced the probability of catastrophic fire (Covington et al. 2001), and have also increased herbaceous standing crop (Moore et al. 2006). However, an important finding in this study is that forest patch types do not respond equally to restoration treatments, at least not within a decade of treatment. Indeed, patch effects were stronger than treatment effects in this project (Table 1; Moore et al. 2006), suggesting that treatment response varies considerably among patches. Patch size and shape are the building blocks of landscape-scale forest structure in this system. This perspective can guide the development of forest structure prescriptions and measurement criteria for other restoration projects where long-term monitoring is implemented. This study suggests that herbaceous standing crop will likely remain low beneath pre-settlement and remaining post-settlement trees within the first decade of a restoration project. If increasing herbaceous production is a primary goal of a restoration effort, then prescriptions that create a heterogeneous forest structure with large openings will maximize success. Because this study was limited to a study site on basalt soils at approximately 2,200 m in elevation, these results should be confirmed on other soil types or in other regions of the pine forest ecosystem; therefore, we caution extrapolating these results to all ponderosa pine forests. Further, monitoring at this long-term research site will continue to assess understory production in all patches, focus on functional group and interspecific differences in response, and address climatic effects on the understory community.

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LITERATURE CITED

- Aguilera, M. O., and W. K. Lauenroth. 1995. Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. *Journal of Ecology* **83**:87–97.

- Aronson, J., S. Dhillon, and E. Le Floch. 1995. On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. *Ecological Restoration* **3**:1–3.
- Avery, C. C., F. R. Larson, and G. H. Schubert. 1976. Fifty-year records of virgin stand development in southwestern ponderosa pine. USDA Forest Service General Technical Report RM-22. USDA Forest Service, Fort Collins, Colorado.
- Bakker, J. D. 2005. Long-term vegetation dynamics of ponderosa pine forests. Ph.D. dissertation, Northern Arizona University, Flagstaff.
- Bakker, J. P., A. P. Grootjans, M. Hermy, and P. Poschlod. 2000. How to define targets for ecological restoration? Introduction. *Applied Vegetation Science* **3**:3–6.
- Baskin, C. C., and J. M. Baskin. 2001. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California.
- Bojorquez Tapia, L. A., P. F. Ffolliott, and D. P. Guertin. 1990. Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. *Journal of Range Management* **43**:25–28.
- Busing, R. T., and P. S. White. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* **78**:562–568.
- Casey, C. A. 2004. Herbaceous biomass and species composition responses to ponderosa pine restoration treatments. M.S. Thesis, Northern Arizona University, Flagstaff, Arizona.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117–143.
- Clary, W. P. 1975. Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge. USDA Forest Service Research Paper RM-158. USDA Forest Service, Fort Collins, Colorado.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* **30**:129–164.
- Covington, W. W., P. Z. Fulé, S. C. Hart, and R. P. Weaver. 2001. Modeling ecological restoration effects on ponderosa pine forest structure. *Restoration Ecology* **9**:421–431.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* **95**:23–29.
- Covington, W. W., and M. M. Moore. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth pine forests. *Journal of Sustainable Forestry* **2**:153–181.
- Dieterich, J. H. 1980. Chimney Spring forest fire history. USDA Forest Service Research Paper RM-220. USDA Forest Service, Fort Collins, Colorado.
- Donath, T. W., N. Hölzel, and A. Otte. 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Journal of Vegetation Science* **6**:13–22.
- Edminster, C. B., and W. K. Olsen. 1996. Thinning as a tool in restoring and maintaining diverse structure in stands of southwestern ponderosa pine. Pages 62–68 in W.W. Covington and P.K. Wagner, technical coordinators. Conference on Adaptive Ecosystem Restoration and Management: Restoration of Cordilleran Conifer Landscapes of North America. USDA Forest Service General Technical Report RM-GTR-278. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Ehrenfeld, J. G. 2000. Defining the limits of restoration: the need for realistic goals. *Restoration Ecology* **8**:2–9.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* **57**:1–32.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57–68.
- Ffolliott, P. F. 1983. Overstory-understory relationships: southwestern ponderosa pine forests. Pages 13–18 in E.T. Bartlett and E.R. Betters, editors. Overstory-understory relationships in western forests. Western Region Research Publication 1. Colorado Agricultural Experiment Station, Fort Collins.
- Forsling, C. L., and W. A. Dayton. 1931. Artificial reseeding on western mountain range lands. U.S. Department of Agriculture Circulation 178. U.S. Department of Agriculture, Washington, D.C.
- Friederici, P., editor. 2003. Ecological restoration of southwestern ponderosa pine forests. Island Press, Washington, D.C.
- Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine. *Ecological Applications* **7**:895–908.
- Fulé, P. Z., W. W. Covington, H. B. Smith, J. D. Springer, T. A. Heinlein, K. D. Huisinga, and M. M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, USA. *Forest Ecology and Management* **170**:19–41.
- Fulé, P. Z., D. C. Laughlin, and W. W. Covington. 2005. Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA. *Forest Ecology and Management* **218**:129–145.
- Goldstein, P. Z. 1999. Functional ecosystems and biodiversity buzzwords. *Conservation Biology* **8**:27–38.
- Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* **4**:93–110.
- Holling, C. S. 1978. Adaptive environmental assessment and management. John Wiley and Sons, London.
- Kerns, B. K., M. M. Moore, M. E. Timpson, and S. C. Hart. 2003. Soil properties associated with vegetation patches in a *Pinus ponderosa*-bunchgrass mosaic. *Western North American Naturalist* **3**:452–462.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**:849–856.
- Laughlin, D. C., J. D. Bakker, M. T. Stoddard, M. L. Daniels, J. D. Springer, C. N. Gildar, A. M. Green and W. W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* **199**: 137–152.
- Leach, M., and T. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* **273**:1555–1558.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* **9**: 228–239.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach, Oregon.
- McLaughlin, S. P. 1978. Overstory attributes, light, throughfall, and the interpretation of overstory-understory relationships. *Forest Science* **24**:550–553.
- Moore, M. M., C. A. Casey, J. D. Bakker, J. D. Springer, P. Z. Fulé, W. W. Covington, and D. C. Laughlin. 2006. Herbaceous response to restoration treatments in a ponderosa pine forest, 1992–2004. *Rangeland Ecology and Management* **59**:135–144.
- Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* **9**:1266–1277.
- Moore, M. M., and D. A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. *Journal of Range Management* **45**:267–271.
- Moore, M. M., D. W. Huffman, P. Z. Fulé, W. W. Covington, and J. E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science* **50**:162–176.

- Moser, E. B., A. M. Saxton, and S. R. Pezeshki. 1990. Repeated measures analysis of variance: application to tree research. *Canadian Journal of Forest Research* **20**:524–535.
- National Oceanic and Atmospheric Administration (NOAA). 2005. URL <http://www.noaa.gov> [accessed 25 January 2005].
- Naumburg, E., and L. E. DeWald. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *Forest Ecology and Management* **124**:205–215.
- Naumburg, E., L. E. DeWald, and T. E. Kolb. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. *Canadian Journal of Botany* **79**:1001–1009.
- Olberding, S. D. 2000. Fort Valley: the beginnings of forest research. *Forest History Today* (Spring): 9–15.
- Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis, 5th edition. Duxbury, Pacific Grove, California.
- Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* **5**:291–300.
- Palmer, M. A., E. S. Bernhardt, J. D. Allan, P. S. Lake, G. Alexander, S. Brooks, et al. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* **42**:208–217.
- Pearson, G. A. 1923. Natural reproduction of western yellow pine in the Southwest. USDA Bulletin No. 1105, Washington, D.C.
- Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando, Florida.
- Riegel, G. M., R. F. Miller, and W. C. Krueger. 1995. The effects of aboveground and belowground competition on understory species composition in a *Pinus ponderosa* forest. *Forest Science* **41**: 864–889.
- Sackett, S. S., and S. M. Haase. 1998. Two case histories for using prescribed fire to restore ponderosa pine ecosystems in northern Arizona. Pages 380–389 in T.L. Pruden and L.A. Brennan, editors. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, Florida.
- SAS Institute, Inc. 2004. JMP-IN ver. 5.1.2. Statistical Analysis Software. SAS Institute, Inc., Cary, NC.
- Schoennagel, T., D. M. Waller, M. G. Turner, and W. H. Romme. 2004. The effect of fire interval on post-fire understory communities in Yellowstone National Park. *Journal of Vegetation Science* **15**: 797–806.
- Snider, G. B., D. B. Wood, and P. J. Daugherty. 2003. Analysis of costs and benefits of restoration-based hazardous fuel reduction: treatment versus no treatment. Progress report # 1, June 13. School of Forestry, Northern Arizona University, Flagstaff. Unpublished report.
- Sydes, C., and S. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. *Journal of Ecology* **69**:249–262.
- Verhagen, R., J. Klooker, J. P. Bakker, and R. van Diggelen. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Applied Vegetation Science* **4**:75–82.
- Vose, J. M., and A. S. White. 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. *Forest Ecology and Management* **40**:175–187.
- White, A. S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* **66**:589–594.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229–299.
- White, P. S., and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology* **5**:338–349.
- Wright, H. A. 1971. Why squirreltail is more tolerant to burning than needle-and-thread. *Journal of Range Management* **24**:277–284.
- Young, J. A., R. A. Evans, C. A. Raguse, and J. R. Larson. 1981. Germinable seeds and periodicity of germination in annual grasslands. *Hilgardia* **49**:1–37.
- Young, R. P., and R. F. Miller. 1985. Response of *Stipanion hystrix* (Nutt.) J.G. to prescribed burning. *American Midland Naturalist* **113**:182–187.