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Forest Ecology and Management 199 (2004) 137–152

Forest Ecology and Management

www.elsevier.com/locate/foreco

Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest

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Received 30 January 2004; received in revised form 6 May 2004; accepted 10 May 2004

Abstract

Remote ponderosa pine (*Pinus ponderosa*) forests on the North Rim of Grand Canyon National Park, Arizona, USA provide valuable examples of reference conditions due to their relatively uninterrupted fire regimes, limited grazing history, and protection from logging. Wildfire is an important disturbance agent in upland forests of the Interior West, yet repeated measurements taken before and after lightning-ignited fires are rare. In 1999, a low-severity Wildland Fire Use fire burned 156 ha on Fire Point, a peninsula dominated by old-growth ponderosa pines, which had not burned for at least 76 years. We measured understory plant community and forest floor characteristics in 1998 (1 year before the fire) and 2001 (2 years after the fire) at this site and at nearby reference sites that did not burn in 1999 but have had continuing fire regimes throughout the past century. After the wildfire, the plant community at Fire Point shifted toward higher compositional similarity with the reference sites. Analysis of functional group composition indicated that this change was due primarily to an increase in annual and biennial forbs. *Gayophytum diffusum*, *Polygonum douglasii*, *Chenopodium* spp., *Solidago* spp., *Elymus elymoides*, *Calochortus nuttallii*, *Hesperostipa comata*, and *Lotus* spp. were indicative of forests influenced by recent fires. Species richness, plant cover, plant layer density and plant diversity were significantly lower at Fire Point than at the reference sites, possibly due to long-term fire exclusion, but the fire did not increase the rate of change in these variables after 2 years. Few exotic species were present at any site. Forest floor depths at Fire Point were reduced to depths similar to the reference sites, primarily due to consumption of the duff layer. There was a significant inverse relationship between the ratio of duff:litter and species richness. Compared to fire-excluded forests, old-growth ponderosa pine forests influenced by low-intensity surface fires generally have greater plant species richness (especially annual forbs) and lighter fuel loads. This study supports the continued application of the Wildland Fire Use strategy in old-growth montane forests to maintain and improve forest health by altering understory species composition and reducing fuel loads.

Keywords: Annuals; BACI design; Fire history; Grand Canyon; Ponderosa pine; Reference conditions; Understory vegetation; Wildland Fire Use

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1. Introduction

Optimal management of ponderosa pine (*Pinus ponderosa*) forest communities hinges on an adequate

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doi:10.1016/j.foreco.2004.05.034

understanding of wildfire effects on forest structure and composition. The effects of stand-replacing fires on herbaceous communities are well documented (e.g. Crawford et al., 2001; Griffis et al., 2001), but the benefits of low-severity wildfires on community composition have received little attention. Ponderosa pine forests in the southwest have been significantly altered since Euroamerican settlement. A variety of factors, including overgrazing (Savage and Swetnam, 1990; Savage, 1991), logging, a favorable climate for pine regeneration (Savage, 1991; Savage et al., 1996), and management practices such as fire suppression, interacted to cause tremendous increases in tree density and fuel loads and reductions in species richness and plant cover (Cooper, 1960; Covington and Moore, 1994a,b; Mast et al., 1999; Allen et al., 2002). Land managers are increasingly interested in managing wildfires under the strategy of Wildland Fire Use to restore degraded forests (Brown et al., 1994; Miller, 2003), but require 'base datum' (Leopold, 1941) information on presettlement conditions and wildfire effects to guide management decisions. The presettlement era is a widely accepted reference point for southwestern ponderosa pine forests because it represents the range of historical 'natural variability' (Landres et al., 1999; Fulé et al., 2002) at a time when critical ecosystem processes, particularly a frequent, low-intensity fire regime, had not been altered by Euroamerican settlers (Agee, 1993; Swetnam and Baisan, 1996; Fulé et al., 1997; Moore et al., 1999).

Dendrochronological methods can examine extant evidence of overstory structure and fire history to determine overstory reference conditions (e.g. Fulé et al., 1997, 2003). The overall conclusion from these studies and from historical accounts (e.g. Woolsey, 1911) is that presettlement forests in the southwest were dominated by an overstory of clumped old-growth ponderosa pines and were subject to frequent low-intensity surface fires. Less information is available concerning understory reference conditions. Historical accounts and early photographs suggest that the understory in southwestern ponderosa pine forests was a diverse bunchgrass-dominated community (Beale, 1858; Rusby, 1889; Merriam, 1890). Currently, floristic diversity and vegetation density are reduced relative to presettlement times, though these changes are difficult to quantify (Arnold, 1950; Covington and Moore, 1994a,b), in part because non-woody material decays rapidly. Therefore, the study of understory reference conditions requires different approaches than can be used for the overstory. These approaches have included modeling of overstory–understory relationships (Covington and Moore, 1994b; Naumburg and DeWald, 1999), phytolith analysis (Kerns et al., 2001), and quantifying the ecosystem characteristics of relict sites (Gildar et al., 2004). In southwestern ponderosa pine forests, relict sites generally contain old-growth trees, have experienced little grazing by domestic livestock (Belsky and Blumenthal, 1997), and have relatively uninterrupted fire regimes (Fulé et al., 2003).

Analyses of wildfire effects are rare because it is difficult to study random events with robust, replicated experiments (van Mantgem et al., 2001). Therefore, most studies of fire effects in ponderosa pine forests have focused on prescribed burns that are more easily controlled and manipulated (e.g. Harris and Covington, 1983; Armour et al., 1984; Andariese and Covington, 1986). However, wildfires (including Wildland Fire Use fires) differ from prescribed burns in timing, intensity, and size. Wildland Fire Use is the management of naturally ignited wildland fires to improve forest health and resources in fire-adapted ecosystems (Miller, 2003). Knowledge about the effects of Wildland Fire Use fires would greatly increase our understanding of the role of fire in ponderosa pine forests and would help guide management decisions. Moreover, data on wildfire effects from relict sites would be especially valuable since these fires would represent effects akin to presettlement processes.

The objectives of this study were to compare an old-growth ponderosa pine forest that has experienced long-term fire exclusion with a broad range of reference sites that have experienced a relatively undisrupted fire regime throughout the past century. Measurements were made before and after a low-severity fire. Analyses were conducted on the understory vegetation (at the community, functional group, and species levels), and on forest floor characteristics. On the basis of these results, we present inferences about fire's role in structuring understory communities and reference conditions.

2. Methods

2.1. Study sites

This study was conducted at the southern extent of the Kaibab Plateau at three remote locations on the North Rim of Grand Canyon National Park (GCNP): Fire Point, Powell Plateau, and Rainbow Plateau (Fig. 1). All three sites are dominated by ponderosa pine, Gambel oak (*Quercus gambelii*), and New Mexico locust (*Robinia neomexicana*). Total basal area was approximately 30 m^2/ha across all sites (Fulé et al., 2002). Common herbaceous species at the sites include *Poa fendleriana*, *Carex geophila*, *Lupinus hillii*, *Eriogonum racemosum*, and *Antennaria parvifolia*. Elevations range from 2225 to 2340 m. Soils have been tentatively classified as Typic Paleustalfs and were derived from Kaibab limestone. These forests have never been commercially harvested (Warren et al., 1982). Evidence exists for limited livestock grazing on the Kaibab Plateau as early as 1871 (Woodbury, 1944) and significant cattle grazing by 1885 (Rasmussen, 1941). However, cattle and sheep grazing essentially ceased in GCNP in the mid-1930s, when a fence was built along the northern boundary of the park to exclude domestic animals. Rasmussen (1941: 253) described the ponderosa pine forests of the Kaibab Plateau as open with "sunlight reach[ing] the ground in almost all parts of the forest".

Average annual precipitation at the Bright Angel ranger station (elevation 2564 m) is 63.7 cm. Average daily temperatures range from a maximum of 25.2 °C in July to a minimum of −8.3 °C in January (Western Regional Climate Center, www.wrcc.dri.edu). 1998 was wetter than average while 2001 was drier than average. In 1998, late winter (January–March) precipitation totaled 35.0 cm (133% of the recorded average precipitation in these months from 1948 to 2003) and early growing season (April–July) precipitation totaled 15.9 cm (129% of average). In 2001, late winter (January–March) precipitation totaled 21.7 cm (83% of average) and early growing season (April–July) precipitation totaled 9.4 cm (76% of average). The study sites are approximately 280 m lower than the weather station and therefore were slightly warmer and drier than the station.

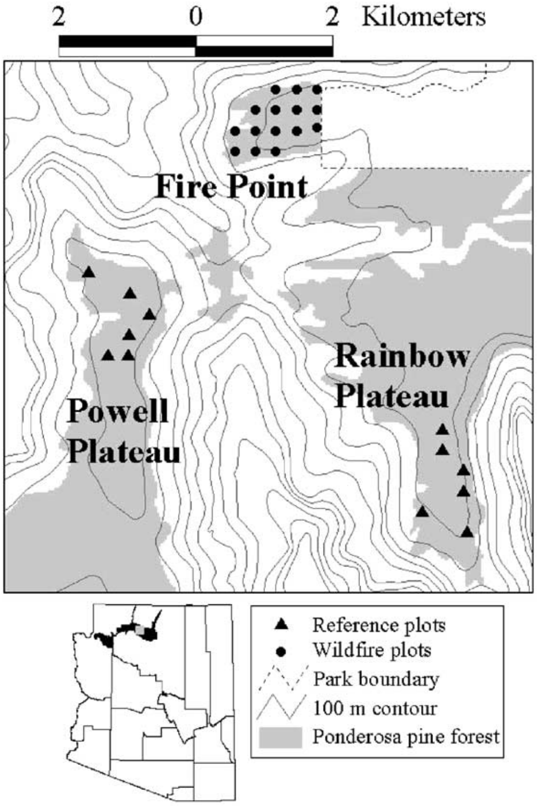

Fig. 1. Study area on the North Rim of Grand Canyon National Park, Arizona, USA. Ponderosa pine forest outside the park is not shown.

Surface fire regimes on the North Rim were interrupted after 1879 (Fulé et al., 2003). Prior to 1880, fire frequency at all three sites ranged from 3.0 to 8.9 years. Most fires occurred relatively late in the growing season. Since 1879, fire frequency was reduced on Rainbow and Powell Plateaus, but each experienced three large fires and several smaller fires. Large fires occurred on Powell Plateau in 1892, 1924, and 1987 and on Rainbow Plateau in 1900, 1985, and 1993 (see Fulé et al. (2003) for dates of small fires). These relatively uninterrupted fire regimes are highly unusual in the southwest (Swetnam and Baisan, 1996); therefore, these sites may have retained key elements of 'wildness' or 'naturalness' (Fulé et al., 2002). On Fire Point, in contrast, the only large fire between 1879 and 1999 occurred in 1923. All of the recording trees that detected this fire were located in the western half of the study area, suggesting that the eastern half of Fire Point did not burn between 1879 and 1999. The three southern-most plots on Fire Point may have also burned in the 'Muav' fire of 1989. On 2 September 1999 a wildfire (the 'Boundary' fire) was ignited by lightning on Fire Point. The low-intensity fire was declared a Wildland Fire Use fire (hereafter, 'wildfire') and was assisted by the National Park Service. It burned a patchy mosaic across 156 ha of the peninsula and was declared out on 12 December 1999. On average, this fire reduced ponderosa pine basal area by <1 m^2/ha (A. Green, unpublished data).

2.2. Data collection

Permanent plots arranged on a systematic 300 m grid were established in 1998 in GCNP to study forest structure, composition, and fire histories across an elevational gradient (for details, see Fulé et al., 2002, 2003). This study focuses on the fifteen plots at Fire Point and six plots at each of Rainbow and Powell Plateaus. All gridded plots on Rainbow and Powell Plateaus were measured in 1998 but 12 plots were remeasured in 2001 and were chosen to represent a range of topographic positions (Gildar et al., 2004). Low sample sizes inhibited rigorous testing of plot independence, but we found no evidence for spatial autocorrelation of plots separated by at least 300 m with Moran's *I*-test. Each plot was 0.1 ha (20 m × 50 m) in size and was oriented with the 50 m sides uphill–downhill to maximize sampling variability along the elevational gradient. Plot corners and centers were permanently marked with 30 cm iron stakes sunk flush to the forest floor and the distance and bearing from a tagged reference tree to the center of the plot was recorded.

Understory vegetation and forest substrates were sampled using belt and point intercept transects. Complete species lists were collected in two 10 m × 50 m belt transects per plot. Each species occurred on zero, one, or two belt transects per plot; these data were used for the analysis of community, functional group, and species responses. We lumped species to the generic level when vegetative characteristics were insufficient to warrant a species-level identification; for example, '*Chenopodium* spp.' includes *C. fremontii*, *C. berlanderii*, and possibly others; '*Lotus* spp.' includes *L. utahensis*, *L. wrightii*, *L. plebius*, and hybrids; and '*Solidago* spp.' includes *S. canadensis*, *S. velutina* and perhaps others. Botanical nomenclature and classification of plant nativity follows US Department of Agriculture Natural Resource Conservation Service, 2004.

A 50 m point intercept transect was established in the center of each belt transect, and species presence and forest floor substrates (soil, litter, rock, wood) were recorded every 30 cm along each transect (166 points per transect). We summed the data from the two transects per plot, yielding a total of 332 points per plot. Percent cover estimates for each plant species (foliar cover) and substrate were calculated by dividing the number of points containing that attribute by the 332 points per plot. All vascular plant species shorter than breast height (1.37 m tall), including trees and shrubs, were included in the analysis. Shannon's H' index of plant diversity was calculated from point intercept data. Overstory canopy cover measured by vertical projection (Ganey and Block, 1994) was recorded along the point intercept transect. Plant layer densities were calculated by averaging the number of plants (layers of plants) detected at each point where at least one plant was recorded.

Forest floor characteristics (litter and duff depth) were measured on three permanent 15.24 m (50 ft) planar transects per plot using the method outlined in Brown (1974). The litter layer (O_i) is composed of freshly fallen organic material, and the duff layer ($O_e + O_a$) is the combined fermentation and humus layers located between the litter layer and mineral soil (Brown, 1974). Forest floor characteristics were sampled in 1998 and 2001 at Fire Point but were only sampled in 1998 at the reference sites.

2.3. Data analysis

This study capitalized on a random disturbance event (wildfire) and therefore could not utilize optimal experimental design techniques such as replication and randomization (van Mantgem et al., 2001). However, our study had a Before-After/Control-Impact (BACI) design (Green, 1979, 1993; Stewart-Oaten and Murdoch, 1986; Underwood, 1994) allowing us to compare the post-wildfire plant community with the community on the same plots prior to fire and with the community on the nearby Rainbow and Powell Plateaus in the same years. Our objective was to compare changed conditions at Fire Point to a broad range of reference conditions. Gildar et al. (2004) concluded that there was great variability in understory reference conditions within Powell and Rainbow Plateaus but there were virtually no significant differences between these sites. Therefore, we combined plots from these two sites for this analysis. Technically, the reference plots are not 'controls' because they are not similar to pre-burn conditions at Fire Point. Rather, they represent 'reference conditions' and are actually more similar to post-burn conditions, as this paper seeks to demonstrate. For clarity and brevity, we refer to pre-fire (1998) data from Fire Point as 'Fire Point-PRE', post-fire (2001) data from Fire Point as 'Fire Point-POST', and the plots on Rainbow and Powell Plateaus as 'reference plots'.

Plots were sampled within a 2 month period in each year due to time constraints imposed by intensive sampling across a large landscape. Fire Point-PRE was measured in early June 1998, Fire Point-POST was measured in early July 2001, and the reference sites were measured from mid-June to mid-July in both years. To account for the different sampling dates at Fire Point, we deleted spring ephemerals (*Claytonia lanceolata* and *Mertensia macdougalii*) that were no longer detectable in July from the community analyses.

We used non-metric multi-dimensional scaling (MDS) to illustrate differences in community composition among sites and years (Clarke, 1993). Non-metric MDS ordinations were conducted using PC-ORD software (Version 4.25; McCune and Mefford, 1999). Non-metric MDS arranges the plots in a configuration that minimizes the inter-plot distances (stress). Unlike principal components analysis and other ordination techniques, the axes in a non-metric MDS plot have no meaning as the interest is in the relationships between plots. 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 100 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 and Grace, 2002).

We used a series of tests to examine whether the reference and Fire Point plots differed from one another in community composition in 1998, in community composition in 2001, and in rate of community change between 1998 and 2001. Site comparisons in 1998 and in 2001 were made with DISTLM software (Version 2.0; Anderson, 2003). This software permits the analysis of univariate or multivariate data using any distance measure and linear model, including multi-factorial ANOVA designs. The calculated statistic is termed a 'pseudo-*F*' and 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 Anderson (2001) and McArdle and Anderson (2001) for details). Data were untransformed and unstandardized. Dissimilarities were calculated using the Bray–Curtis distance measure as this distance measure is appropriate for most ecological data (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.

Comparisons of rate of change between 1998 and 2001 required that we account for autocorrelation between repeated measurements of permanent plots. Some authors have suggested that repeat measurements be analyzed as a 'split-plot in time' (e.g. Steel and Torrie, 1960), but split-plot analyses assume that the data are uncorrelated. Failure to account for autocorrelation in the analysis may lead to differences being declared significant more often than they truly are significant. Univariate analyses can use a Greenhouse–Geisser or Huynh–Feldt adjustment to account for autocorrelation (Moser et al., 1990), but these adjustments have not been extended to multivariate analyses. Instead, we accounted for autocorrelation between repeated measurements by calculating the multivariate dissimilarity (Bray–Curtis distance) between the 1998 and 2001 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 Wilcoxon 2-sample test; a significant result indicated that the site with greater dissimilarity experienced a greater change in community composition between 1998 and 2001.

We followed these tests of overall community response by tests of individual functional groups to see whether changes were occurring in all or in a subset of the functional groups. Four functional groups were identified: annual and biennial forbs (8 of 10 species in this group were annuals), perennial forbs, graminoids, and woody species (shrubs and tree seedlings below breast height). The three tests described above (testing for differences between reference and Fire Point plots in community composition in 1998, in community composition in 2001, and in rate of community change between 1998 and 2001) were conducted on the composition of each functional group. We also used the multivariate technique to test the multivariate response of functional group species richness (i.e. number of annual and biennial forbs, number of perennial forbs, etc.).

To test the overall response of species richness 0.1 ha^{-1}, we calculated the total number of species on each plot (including those species omitted from analyses of community composition; see McCune and Grace (2002)) and tested whether reference and Fire Point plots differed in species richness in 1998, species richness in 2001, and rate of change of species richness between 1998 and 2001. Since these analyses involved univariate response variables, the dissimilarities between 1998 and 2001 were simply the differences between the two species richness values for each plot. We followed these tests of overall species richness by tests of species richness of each functional group to see whether changes were occurring in all functional groups or in a subset of them. Additional univariate tests were conducted for plant cover, plant layer density, plant diversity (Shannon's H'), and percentage of native species. We used Wilcoxon 2-sample tests for comparisons between sites in 1998, in 2001, and of rate of change between sites.

We used the indicator species analysis (ISA; Dufrêne and Legendre, 1997) routine in PC-ORD to identify individual plant species associated with particular sites and/or years. A hierarchical approach compared sites and then years within sites. Species were considered indicators of the site 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 1000 permutations) and INDVAL >25. Since INDVAL is the product of the relative abundance and relative frequency of a species, a species could have an INDVAL of 25 if, for example, it occurred on 50% of the plots within a group and had a relative abundance of at least 50% across all groups (Dufrêne and Legendre, 1997). For each site-year, relative abundance was calculated as the percentage of belt transects in which a species was detected and relative frequency was calculated as the percentage of plots in which a species was detected.

Since frequencies of forest floor substrates (litter, rock, soil, wood) are correlated with one another, we analyzed them using the multivariate procedure described above for community composition. Forest floor fuels data had unequal variances, so we used the same non-parametric methods utilized above for univariate community data. Forest floor fuels from Fire Point-PRE and the references sites in 1998 were analyzed with Wilcoxon 2-sample tests. Pre and post-fire fuels data from Fire Point were analyzed with Wilcoxon signed ranks tests (Conover, 1999). We were unable to compare the rate of change between sites because fuels were not measured at the reference plots in 2001. We also used linear regression to examine the relationship between species richness and forest floor fuels (litter depth, duff depth, total forest floor depth, and duff:litter ratio). Regressions were developed using pre-fire (1998) data from Fire Point and the reference sites.

3. Results

3.1. Understory plant community

A total of 118 species were identified across all sites and years. The analysis of community composition focused on the 70 species that occurred on at least 5% of the plots. Sites differed in composition in both 1998 and 2001, though the magnitude of the difference diminished over time (Table 1). Between 1998 and 2001, the community changed significantly more at Fire Point than at the reference sites (Table 1). The non-metric MDS ordination illustrated this result by grouping Fire Point-PRE plots together but showing little difference between Fire Point-POST and reference plots (Fig. 2).

The compositions of all functional groups differed between sites in 1998 but only the perennial forb and woody plant functional groups differed between sites in 2001 (Table 1). The annual and biennial forb community changed at a significantly greater rate at Fire Point than at the reference sites (Table 1); the rate of change for the other functional groups did not differ between sites.

Table 1
Summary statistics of multivariate and univariate analyses comparing the understory communities at the reference sites and Fire Point in 1998 and 2001[a]

	Difference between sites in 1998	Difference between sites in 2001	Difference between sites in rate of change
Species composition			
Community composition[b]	Pseudo-$F = 7.3$, $P <$ **0.001**	Pseudo-$F = 2.7$, $P =$ **0.004**	$Z = -2.3$, $P =$ **0.019**
Functional group composition			
Annual and biennial forbs	Pseudo-$F = 5.4$, $P <$ **0.001**	Pseudo-$F = 1.3$, $P = 0.300$	$Z = -2.3$, $P =$ **0.020**
Perennial forbs	Pseudo-$F = 8.0$, $P <$ **0.001**	Pseudo-$F = 2.3$, $P =$ **0.017**	$Z = -1.3$, $P = 0.196$
Graminoids	Pseudo-$F = 6.4$, $P =$ **0.002**	Pseudo-$F = -0.3$, $P = 0.991$	$Z = -1.2$, $P = 0.221$
Woody plants	Pseudo-$F = 3.1$, $P =$ **0.021**	Pseudo-$F = 4.3$, $P =$ **0.003**	$Z = -0.8$, $P = 0.433$
Species richness			
Functional group species richness[c]	Pseudo-$F = 10.7$, $P <$ **0.001**	Pseudo-$F = 7.7$, $P =$ **0.002**	$Z = -2.9$, $P =$ **0.004**
Annual and biennial forbs	$Z = 2.9$, $P =$ **0.004**	$Z = 0.8$, $P = 0.414$	$Z = -2.3$, $P =$ **0.019**
Perennial forbs	$Z = 3.2$, $P =$ **0.002**	$Z = 2.6$, $P =$ **0.009**	$Z = -1.6$, $P = 0.115$
Graminoids	$Z = 2.0$, $P =$ **0.043**	$Z = 2.1$, $P =$ **0.036**	$Z = -0.3$, $P = 0.779$
Woody plants	$Z = 1.6$, $P = 0.101$	$Z = 2.9$, $P =$ **0.004**	$Z = 1.9$, $P = 0.063$
Substrate frequencies	Pseudo-$F = 1.5$, $P = 0.217$	Pseudo-$F = 0.7$, $P = 0.510$	$Z = -0.4$, $P = 0.714$

[a] See methods for details of analysis techniques. Pseudo-F statistics indicate multivariate analyses and Z statistics indicate univariate analyses. Bold P-values indicate statistically significant results.

[b] Community composition is illustrated in Fig. 2.

[c] Functional group species richness is shown in Fig. 3.

All 118 species were included in the analysis of species richness. Functional group species richness differed between sites in both 1998 and 2001 but changed significantly more at Fire Point than at the reference sites (Table 1). Species richness was significantly higher at the reference sites than at Fire Point in both 1998 and 2001 (Fig. 3), though the rate of change in species richness did not differ between sites (Table 2). Species richness of annual and biennial forbs differed between sites in 1998 but not in 2001 (Table 1 and Fig. 3). Between 1998 and 2001, annual and biennial forb richness increased more at Fire Point than at the reference sites (mean increase = 3.1 and 1.8 species, respectively; Fig. 3). Species richness of perennial forbs and of graminoids was significantly lower at Fire Point than at the reference sites in both 1998 and 2001, though their rates of change did not differ between sites (Table 1 and Fig. 3).

Reference plots had significantly higher plant cover and plant layer density than Fire Point plots in both years (Table 2). Plant diversity (Shannon's H') was higher at the reference sites in 1998, but only marginally higher in 2001. A higher percentage of the species were native at the reference sites than at Fire Point in 1998, though these sites did not differ in percent native species in 2001. Rates of change in these variables did not differ between sites.

3.2. Indicator species analyses

The ISA identified 14 indicator species for the reference sites and three indicator species for Fire Point (Table 3). No species were indicators of the reference sites in 1998 or 2001. One species was identified as an indicator of Fire Point-PRE and eight species as indicators of Fire Point-POST. Most indicators of Fire Point-POST were also common at the reference sites.

3.3. Substrates and forest floor fuels

Substrate frequencies did not vary among sites in 1998 or 2001 or in the rate of change between sites (Table 1). The average substrate frequencies across all sites and years were 92% litter, 1% rock, 4% soil, and 3% wood.

Before the fire, duff depth, total forest floor depth, and the duff:litter ratio (D:L) were significantly higher

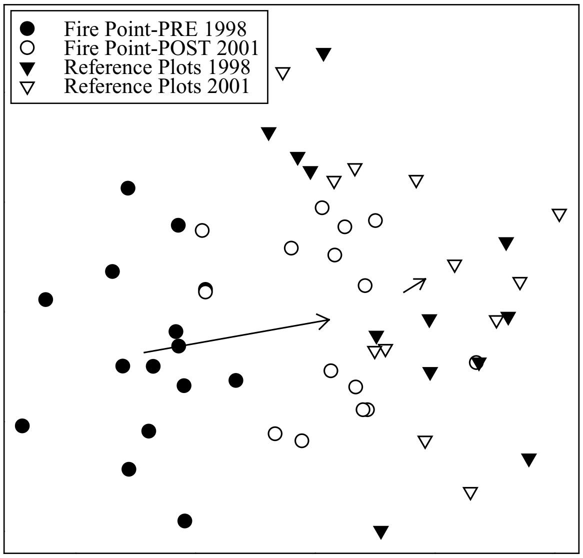

Fig. 2. Non-metric multi-dimensional scaling (MDS) plot of understory plant communities on the North Rim of Grand Canyon National Park, USA. Individual symbols represent individual plots in 1998 and 2001 (solid and hollow symbols, respectively). Arrows connect the centroids (average position within each site-year) of each site in 1998 and 2001 and illustrate the large change at Fire Point. This configuration was determined using the abundances of 70 species on 27 plots in each of 1998 and 2001; the final solution had three dimensions. Stress = 16.5; $P = 0.010$.

at Fire Point than at the reference sites (Table 4). The wildfire significantly increased litter depth and significantly decreased duff depth at Fire Point, with the net result being a significant reduction in total forest floor depth. The fire consumed an average of 2.4 cm (66%) of duff across Fire Point. Post-fire total forest floor depth at Fire Point was similar to that at the reference sites in 1998. The fire also significantly reduced D:L at Fire Point.

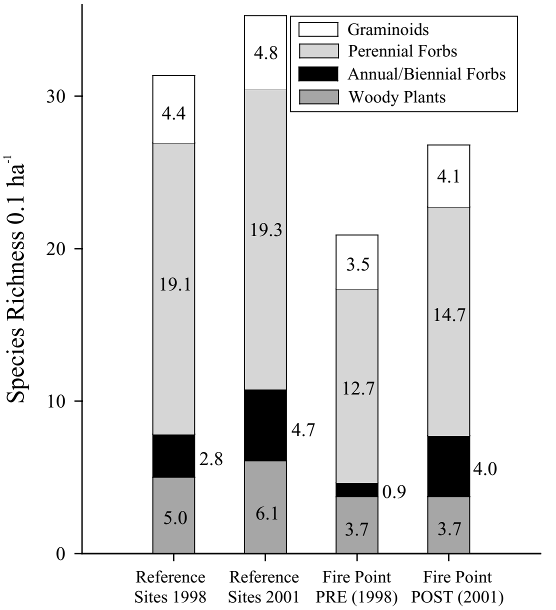

Fig. 3. Mean richness of functional groups at each site in each year.

There was a significant negative relationship ($r^2 = 0.46, P = 0.001$) between D:L and species richness (Fig. 4). The next most significant explanatory variable was duff depth ($r^2 = 0.25$, $P = 0.008$); total forest floor and litter depths were marginally significant ($0.05 < P < 0.1$). However, multiple regression indicated that duff, litter, and total forest floor depth were not significant if D:L was already in the model.

Table 2
Plant community characteristics (mean ± S.D.) at references sites and Fire Point in 1998 and 2001[a]

Community characteristic	Reference sites (1998)	Reference sites (2001)	Fire Point-PRE (1998)	Fire Point-POST (2001)
Species richness 0.1 ha^{-1}	31.3 ± 6.5	34.9 ± 3.8	20.9 ± 6.0	26.5 ± 7.9
Plant cover (%)	34 ± 2	22 ± 2	15 ± 3	16 ± 4
Plant layer density[b]	1.18 ± 0.10	1.14 ± 0.10	1.04 ± 0.05	1.07 ± 0.09
Shannon's H'	2.1 ± 0.2	2.0 ± 0.4	1.8 ± 0.5	1.6 ± 0.6
Percentage of native species 0.1 ha^{-1}	94.1 ± 0.9	94.6 ± 0.3	93.0 ± 0.1	93.6 ± 0.3

[a] See methods for details of analysis techniques. Sites differed in 1998 for all variables ($Z > 2.7$, $P < 0.01$) and in 2001 for all variables ($Z > 2.1$, $P < 0.05$) except Shannon's H' ($Z = -1.9$, $P = 0.057$) and percentage of native species ($Z = 1.0$, $P = 0.341$). There were no differences in rate of change between sites for any variable ($Z < -1.9$, $P > 0.05$).

[b] See methods for calculation of plant layer density.

Table 3
Indicator species associated with sites (reference vs. Fire Point) and years within sites (1998 vs. 2001)[a]

Species	INDVAL[b]	*P*	Reference sites		Fire Point	
			1998	2001	PRE	POST
Reference sites (1998 + 2001)						
Achillea millefolium	49.5	0.004	**58–75**	**50–67**	23–33	23–27
Arabis drummondii	58.4	0.000	**54–75**	**42–58**	–	7–13
Artemisia carruthii	58.7	0.000	**46–58**	**59–67**	–	9–13
Bromus tectorum	37.2	0.014	**34–58**	**25–42**	13–20	10–13
Ceanothus fendleri	57.7	0.001	**50–67**	**54–92**	24–40	20–40
Crepis intermedia	33.3	0.001	**21–33**	**17–33**	–	–
Ericameria nauseosa	30.9	0.035	**29–33**	**38–50**	3–7	20–27
Hymenopappus filifolius	31.3	0.012	**34–42**	**34–33**	–	14–27
Machaeranthera canescens	47.3	0.002	**38–58**	**46–67**	7–13	20–33
Mahonia repens	43.7	0.010	**47–58**	**59–67**	27–33	24–27
Penstemon barbatus	29.6	0.019	**17–25**	**33–50**	3–7	10–13
Penstemon linarioides	43.6	0.012	**46–58**	**54–67**	10–13	34–47
Phacelia egena	37.5	0.000	**42–50**	**25–25**	–	–
Quercus gambelii	63.2	0.000	**71–83**	**92–100**	30–33	44–53
Fire Point (1998 + 2001)						
Agoseris glauca	55.1	0.027	84–83	46–53	**87–100**	**64–87**
Hieracium fendleri	41.2	0.012	4–8	21–33	**37–60**	**30–53**
Lithophragma tenellum	56.9	0.001	17–25	25–33	**74–87**	**47–67**
Reference sites (1998)						
No indicator species	–	–	–	–	–	–
Reference sites (2001)						
No indicator species	–	–	–	–	–	–
Fire Point-PRE (1998)						
D. nuttalianum	57.1	0.037	67–83	54–100	**94–100**	70–93
Fire Point-POST (2001)						
Calochortus nuttallii	73.3	0.000	42–67	38–58	–	**57–73**
Chenopodium spp.	66.7	0.000	21–33	38–58	–	**50–67**
Elymus elymoides	60.4	0.009	96–100	92–100	64–80	**97–100**
G. diffusum	86.7	0.000	29–33	54–67	–	**64–87**
Hesperostipa comata	40.0	0.018	4–8	21–42	–	**30–40**
Lotus spp.	93.3	0.000	79–83	75–83	–	**44–60**
Polygonum douglasii	89.3	0.000	54–67	71–92	4–7	**74–93**
Solidago spp.	54.0	0.013	63–75	54–58	14–20	**57–67**

[a] Analyses comparing Fire Point (15 plots) to reference sites (12 plots) included data from both years. Analyses comparing years within sites did not include data from the other site. The data for each species for each site-year are the percentage of belt transects (%) and the percentage of plots (%) in which the species was detected. For example, *Achillea millefolium* occurred on 58% of belt transects and 75% of plots on the reference sites in 1998. Bold text indicates the site or year within site with which a species was most strongly associated.

[b] INDVAL (indicator value) = relative abundance × relative frequency (see Dufrêne and Legendre (1997) for details of calculation). *P*-values are the proportion of 1000 randomized trials with INDVAL equal to or exceeding the observed INDVAL.

4. Discussion

4.1. Community response

The relict sites on Rainbow and Powell Plateaus provide an excellent benchmark against which to compare the effects of the Boundary Fire at Fire Point because these sites are close together (Fig. 1) and have similar soils, elevations, precipitation patterns, and old-growth conditions. Rainbow and Powell Plateaus span a range of natural variability. Therefore, pre-fire differences at Fire Point demonstrate its departure

Table 4
Forest floor characteristics (mean ± S.D.) at the reference sites in 1998 and at Fire Point in 1998 and 2001[a]

Forest floor fuels	Reference sites (1998)	Fire Point-PRE (1998)	Fire Point-POST (2001)	Fire Point-PRE vs. POST	Fire Point-PRE vs. reference sites (1998)
Litter (O_i) (cm)	0.89 ± 0.8	0.58 ± 0.2	1.32 ± 0.4	$T^+ = 60$, $P <$ **0.001**	$Z = 0.2$, $P = 0.864$
Duff ($O_e + O_a$) (cm)	2.00 ± 0.9	3.67 ± 1.6	1.24 ± 0.5	$T^+ = -60$, $P <$ **0.001**	$Z = -2.8$, $P =$ **0.005**
Total forest floor (cm)	2.89 ± 1.3	4.25 ± 1.7	2.55 ± 0.8	$T^+ = -60$, $P <$ **0.001**	$Z = -2.1$, $P =$ **0.040**
Duff:litter	3.41 ± 2.1	6.70 ± 2.6	1.01 ± 0.5	$T^+ = -60$, $P <$ **0.001**	$Z = -3.0$, $P =$ **0.002**

[a] See methods for details of analysis techniques. Bold *P*-values indicate statistically significant results.

from the local range of variability likely caused by fire exclusion.

The change in community composition between Fire Point-PRE and Fire Point-POST is due at least in part to the wildfire since the rate of compositional change was greater at Fire Point than at the reference sites (Table 1). The wildfire appears to have directed the community composition of Fire Point on a trajectory toward higher similarity with that of the reference plots (see arrows connecting centroids in Fig. 2). In other words, the fire changed the community composition of Fire Point to more closely approximate that of a forest influenced by a relatively frequent fire regime. Additional fires might continue to move the community on a trajectory toward reference conditions. Alternatively, if an extended period of time elapses before the next wildfire at Fire Point, it is conceivable that the community composition might revert back towards the community evident under fire exclusion (Fire Point-PRE). Fire exclusion has been shown to alter species composition in the overstory, primarily due to encroachment by fire-intolerant trees (Dickman, 1978); similar changes likely also occur in the understory but have received little attention.

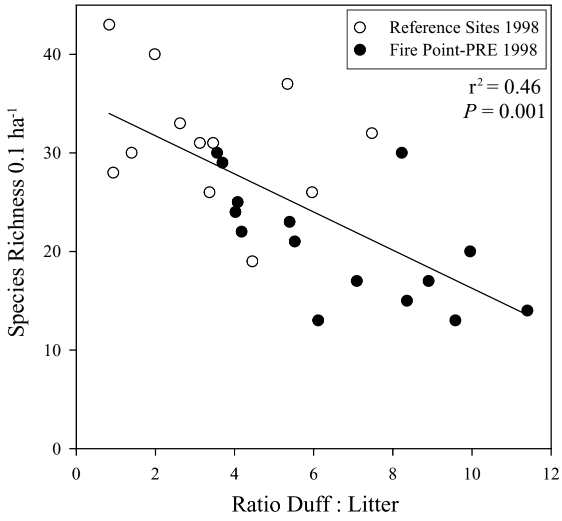

Fig. 4. Relationship between duff:litter ratio and species richness.

The change in community composition was due in part to changes in the annual and biennial forb functional group (Table 1, Fig. 3). Annual and biennial forb species richness was low at Fire Point prior to the fire but increased after the fire to values similar to the reference sites (Table 1, Fig. 3). Fluctuations in annual populations are often associated with wet years, but this was apparently not the case here as the sites received less winter and early growing season precipitation in 2001 than in 1998 (see Section 2). Annual and biennial forb species commonly respond favorably to fire (Barney and Frischknecht, 1974; Young and Evans, 1978; Merrill et al., 1980; Crawford et al., 2001), likely due to the reduction in duff depth and increased availability of microsites for germination.

These results suggest that annual and biennial species are an important component of understory reference conditions in ponderosa pine forests. Forests where fire has been a frequent disturbance agent throughout the past century may maintain high annual and biennial species richness, suggesting that this functional group might serve as an indicator of forest health. The role of this functional group in the ecological community is poorly understood. Further research into the ecology of annual plants in ponderosa pine forests and their potential role as indicators of forest health is warranted.

The change in the annual and biennial forb community at Fire Point was not a shift toward exotic ruderals as has been observed following high-intensity wildfires in northern Arizona (Crawford et al., 2001;

Griffis et al., 2001). Exotics were also not abundant after a prescribed fire in mixed conifer forest on the North Rim of GCNP (Huisinga et al., submitted for publication). The low abundance of exotic species is likely due to the remote location of the North Rim and to long-term protection by the National Park Service. *Bromus tectorum*, *Lactuca serriola*, and *Tragopogon dubius* were the only exotic species detected in this study. *B. tectorum* was more abundant at the reference sites (Table 3), likely due to the proximity of hiking trails to these sites (Gildar et al., 2004) and to more suitable seedbeds created by a continuing fire regime. Recent evidence indicates that bison behavior may be influencing *B. tectorum* populations on Rainbow Plateau (J. Crawford, unpublished report). *B. tectorum* may become an increasing problem in the southwest as frequent, low-intensity fire regimes are reintroduced to large areas; further research is necessary.

The compositional difference between Fire Point-PRE and POST (Fig. 2) could be seen as an artifact of the earlier sampling date. However, the rate of community change between sites was significant (Table 1) even though we omitted spring ephemerals from the community analysis (see Section 2); inclusion of spring ephemerals increased the statistical difference between the pre- and post-burn measurements (data not shown). Sampling date might also influence the abundance of annual forbs at Fire Point-PRE (Fig. 3); however, we feel that this is not a factor since we collected several annual species simultaneously with sampling at Fire Point-PRE. For example, we collected *Chenopodium* spp., *Gayophytum diffusum* and *Polygonum douglasii* in late May to mid-June 1998 from other locations in the region; therefore, these species were alive and growing during sampling and would have been detected if present. Moreover, these annual species commonly increase after fires (see below). Furthermore, the other non-annual indicator species of Fire Point-POST (Table 3) are easily detected from early June to July so sampling date would not affect detection of these species. Though the magnitude of the difference is obscured by sampling date, the direction of the change is certain. We feel that wildfire effects are more significant than sampling date effects in this study.

In comparison to the reference sites, Fire Point had lower species richness, plant cover, plant layer densities, and plant diversity (Table 2). Low species richness and lack of herbaceous cover have also been noted in other ponderosa pine forests after decades of fire suppression (Covington and Moore, 1994a,b). Other studies have demonstrated an increase in herbaceous production over time after fires (Campbell et al., 1977; Oswald and Covington, 1984; Andariese and Covington, 1986). It may take more time, or more fires, to increase species richness and plant cover at Fire Point to levels approaching those at the reference sites.

Fulé et al. (2003) demonstrated that a fire occurred on the western portion of Fire Point in 1923 while the eastern portion likely did not burn between 1879 and 1999. Plots on the western portion of Fire Point were also more similar in species composition to the reference plots than plots on the eastern side of Fire Point: black circles to the right of the Fire Point-PRE centroid in Fig. 2 represent plots from the western portion of Fire Point and black circles to the left of the centroid represent plots from the eastern portion of the site. This suggests that plots that burned in 1923 were more similar to the reference plots than were plots that last burned in 1879. Moreover, average pre-fire annual and biennial richness was lower on the eastern plots (0.3 species per plot) than the western plots (1.5 species per plot). Average species richness was also lower on the eastern plots (15.6 species per plot) than the western plots (25.5 species per plot). Therefore, species richness appears to be influenced by time since the last fire.

4.2. Individual species responses

Some species were indicators of particular sites while other species were indicators of pre- or post-fire conditions at Fire Point (Table 3). Fourteen species were most strongly associated with the reference sites and three species were most strongly associated with Fire Point. Analysis of additional sites would be necessary to determine whether these species are indicative of these sites because of their differing fire histories or because of other conditions (e.g. edaphic) at the sites. The absence of indicator species of the reference sites in 1998 or 2001 provides further support that the reference sites experienced little change between years.

Delphinium nuttalianum, the only indicator of Fire Point-PRE, was more abundant before than after the fire (present in 94% versus 70% of the belt transects at

Fire Point-PRE and POST, respectively) but occurred at similar frequencies before and after the fire (present in 100% versus 93% of the plots, respectively; Table 3). *D. nuttalianum* also occurred on the reference plots at abundances and frequencies comparable to Fire Point-POST, suggesting that fire reduced its abundance but not its frequency. Known fire effects on *Delphinium* spp. are lacking, though *D. bicolor* and *D.* × *occidentale* are probably killed by most fires (Matthews, 1993).

Eight species were indicators of post-fire conditions at Fire Point. These species were also abundant and frequent at the reference sites (Table 3), and contributed to the similarity between Fire Point-POST and the reference sites (Fig. 2). This suggests that these species represent indicators of recently burned ponderosa pine forests on the North Rim.

Several annuals, most notably *G. diffusum*, *Polygonum douglasii*, and *Chenopodium* spp., were absent or infrequent before the fire but abundant afterwards (Table 3). *G. diffusum* was strongly favored by conditions after burning in red fir forests in the Sierra Nevadas (Kilgore, 1971) and also increased after wildfire in other Arizona ponderosa pine forests (Beaulieu, 1975). *Polygonum* spp. are well known for their ability to vigorously sprout from seed after fires (Ahlgren, 1960; Billings, 1969; Beaulieu, 1975). In sagebrush-grasslands in northern Idaho, *P. douglasii* biomass was four times greater in severely burned areas than unburned areas (Blaisdell, 1953). *Chenopodium* spp. are also well known for their adaptations to disturbed environments. *C. album* and *C. leptophyllum* increased in frequency after a fire in a Gambel oak woodland (Poreda and Wullstein, 1994), and *C. album* increased tremendously after severe fires in northern Arizona (Beaulieu, 1975; Crawford et al., 2001).

Solidago spp. are perennial forbs that are well known for their fire tolerance and are diverse in fire prone systems like tallgrass prairie. *S. canadensis* responded positively to low and moderate severity burns (Richards and Landers, 1973; Medve, 1984) and maintained long-term abundance in Gambel oak woodlands that burned (McKell, 1950). Other *Solidago* spp. exhibit positive responses to fire as well (Pase and Knipe, 1977; Anderson and Bailey, 1980; Rabinowitz, 1981).

Elymus elymoides, a perennial grass, can survive in a wide variety of habitats, including dense stands of pine, but also responds favorably to fire. *E. elymoides* was a major component of a post-fire pinôn-juniper woodland in the Great Basin (Koniak, 1985) and also increased in abundance after fires in ponderosa pine forests in Arizona (Beaulieu, 1975; Vose and White, 1991). Prescribed fire increased inflorescence biomass in *E. elymoides* (Young and Miller, 1985). Wright (1971) determined that *E. elymoides* is tolerant of fire because its low biomass burns quickly, preventing heat from penetrating to the meristems.

Calochortus nuttallii, *Hesperostipa comata*, and *Lotus* spp. were indicators of Fire Point-POST but their abilities to tolerate fire are less clear in the literature. Fire appears to be important for *C. nitidus* in open woodlands and grasslands in Idaho (Mancuso and Moseley, 1994); the deeply buried perennial bulbs of *Calochortus* spp. are likely well-protected from fire. Autumn fires (such as this one) damage *H. comata* far less than spring and summer burns (Wright and Klemmedson, 1965; Wright, 1970). *Lotus* spp. increased after fires in Arizona ponderosa pine forests (Beaulieu, 1975).

4.3. Fuel load reduction

The most significant and predictable effect of the wildfire on forest floor fuels was a significant reduction in forest floor depth (Table 4). After at least 76 years of fire exclusion, the forest floor at Fire Point averaged 4.3 cm deep. Another fire-excluded ponderosa pine stand on Galahad Point had an average forest floor depth of 5.6 cm (Gildar et al., 2004). The wildfire on Fire Point reduced the mean forest floor depth by 40%. The total reduction in forest floor depth was entirely due to duff consumption, since litter depth increased after the fire due to needle fall from fire-scorched trees (Table 4). Post-fire and reference site duff depths were within the range (<2 cm) predicted by a model simulating cumulative fire effects in ponderosa pine/Douglas-fir forests (Keane et al., 1990).

The accumulation of duff during years of fire exclusion can negatively impact the plant community. The D:L explained more of the variation of species richness than any other forest floor variable (Fig. 4), suggesting that there is an interactive effect of duff and litter depth on the plant community. Species richness declined as duff depth increased relative to litter depth

(Fig. 4). In theory, therefore, species richness could still be high if litter depths are greater than duff depths. Of course, species richness is also related to other environmental factors, such as arbuscular mycorrhizal inoculum potential (AMIP), canopy cover (Huisinga et al., submitted for publication) and tree densities, but many of these variables are also correlated with duff depth (AMIP is significantly negatively related to duff depth; Gildar, 2002). Wildfires that reduce duff depths and D:L should eventually allow for an increase in plant species richness.

4.4. Reference conditions and ecosystem management

The increasing size and scope of ecological restoration efforts throughout the southwest are magnifying the need to understand understory reference conditions of southwestern ponderosa pine forests. The vast majority of plant diversity in this system is found in the understory and the herbaceous layer provides cover and forage for many native animals (Friederici, 2003). Covington and Moore (1994b) estimated herbage production to be almost four times greater in 1901 than in 2001 within Arizona ponderosa pine forests. Other recent studies regarding understory reference conditions concluded that grasses were more prevalent in historical times near Flagstaff, Arizona (Kerns et al., 2001) and that grasses are more abundant in old-growth forests than in dense stands (Naumburg and DeWald, 1999). Based on analysis of soil phytolith assemblages from locations south of the Grand Canyon, Kerns et al. (2001) concluded that C_4 plants were once more widespread than at present but were still likely less abundant than C_3 plants. We found very few C_4 grasses on the North Rim: only 3 of the 12 grasses detected were C_4, and these three species were detected on <7% of the plots. Perhaps C_3 grasses are better adapted to the generally cooler and wetter pine forests of the North Rim, and C_4 grasses were never dominant in these specific pine forests.

Remote old-growth forests on Powell and Rainbow Plateaus provide valuable examples of reference conditions for North Rim ponderosa pine forests. Understory communities in ponderosa pine forests exhibit a range of variability throughout space and time. In general, however, North Rim forests with continuing fire regimes are characterized by a high proportion of native species, high plant cover (Table 2), low fuel loads (Table 4), and a diversity of species (Table 2) from various functional groups (Fig. 3), especially annual and biennial forbs. We suggest that these characteristics can be used as benchmarks for assessing the success of restoration projects (Christensen et al., 1996) designed to restore presettlement reference conditions in ponderosa pine forests on the North Rim. Reference conditions in North Rim forests likely differ from reference conditions in other southwestern forests with differing moisture regimes, soils, and bedrock (Gildar et al., 2004). Extrapolation of data from these sites to other biogeographical regions should be made cautiously and must recognize inherent site differences.

Fire is an extremely important process in western forests (Agee, 1993) and can play an essential role in restoring reference conditions to certain forest types (Stephenson, 1999). This study demonstrates that a wildfire that was allowed to burn in an old-growth ponderosa pine forest directed the understory community towards that found on reference sites by shifting the species composition and reducing fuel loads. This suggests that the Wildland Fire Use strategy is a useful management tool for directing understory communities toward reference conditions. We recommend that land managers continue to allow lightning-set, low-intensity fires to burn in old-growth forests to encourage forested landscapes to remain within the historic range of variability.

Acknowledgements

We thank P. Fulé for reviewing the manuscript and the many staff and students of the Ecological Restoration Institute for assistance with data collection. We also thank M.J. Anderson of the University of Auckland and the Statistical Consulting Lab at Northern Arizona University for statistical advice. This work was funded by grants from the National Park Service and Bureau of Land Management.

References

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Ahlgren, C.E., 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology 41, 431–445.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol. Appl. 12, 1418–1433.

Andariese, S.W., Covington, W.W., 1986. Changes in understory production for three prescribed burns of different ages in ponderosa pine. For. Ecol. Manage. 14, 193–203.

Anderson, H.G., Bailey, A.W., 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. Can. J. Bot. 58, 985–996.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Aust. Ecol. 26, 32–46.

Anderson, M.J., 2003. DISTLM v.2: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. Department of Statistics, University of Auckland, New Zealand.

Armour, C.D., Bunting, S.C., Neuenschwander, L.F., 1984. Fire intensity effects on the understory in ponderosa pine forests. J. Range Manage. 37, 44–49.

Arnold, J.F., 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. J. For. 48, 118–126.

Barney, M.A., Frischknecht, N.C., 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. J. Range Manage. 27, 91–96.

Beaulieu, J.T., 1975. Effects of fire on understory plant populations in a northern Arizona ponderosa pine forest. Thesis. Northern Arizona University, Flagstaff, AZ, 38 pp.

Beale, E.F., 1858. Wagon road from Fort Defiance to the Colorado River. In: 35th Congressional Session, Senate Executive Document 124.

Belsky, A.J., Blumenthal, D.M., 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. Conserv. Biol. 11, 315–327.

Billings, W.D., 1969. Vegetational pattern near alpine timberline as affected by fire–snowdrift interactions. Vegetatio 19, 192–207.

Blaisdell, J.P., 1953. Ecological effects of planned burning of sagebrush-grass range on the upper Snake River Plains. Tech. Bull. 1975. US Department of Agriculture, Washington, DC, 39 pp.

Brown, J.K., 1974. Handbook for Inventorying Downed Woody Material. USDA For. Serv. Gen. Tech. Rep. INT-16. Intermountain Forest and Range Experiment Station, Ogden, UT.

Brown, J.K., Arno, S.F., Barrett, S.W., Menakis, J.P., 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. Int. J. Wildland Fire 4, 157–168.

Campbell, R.E., Baker, M.B., Ffolliott, P.F., Larson, F.R., Avery, C.C., 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. US Department of Agriculture, Forest Service Research Paper RM-191.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., Woodmansee, R.G., 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecol. Appl. 6, 665–691.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Conover, W.J., 1999. Practical Nonparametric Statistics. Wiley, New York, NY.

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

Covington, W.W., Moore, M.M., 1994a. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. J. Sustain. For. 2, 153–181.

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

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

Dickman, A., 1978. Reduced fire frequency changes species composition of a ponderosa pine stand. J. For. 76, 24–25.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Friederici, P. (Ed.), 2003. Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, DC.

Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine. Ecol. Appl. 7, 895–908.

Fulé, P.Z., Covington, W.W., Moore, M.M., Heinlein, T.A., Waltz, A.E.M., 2002. Natural variability in forests of the Grand Canyon, USA. J. Biogeogr. 29, 31–47.

Fulé, P.Z., Heinlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. Int. J. Wildland Fire 12, 129–145.

Ganey, J.L., Block, W.M., 1994. A comparison of two techniques for measuring canopy closure. West. J. Appl. For. 9, 21–23.

Gildar, C.N., 2002. Plant community and arbuscular mycorrhizal dynamics have implications for determining ponderosa pine reference conditions. MS Thesis. Northern Arizona University, Flagstaff, Arizona.

Gildar, C.N., Fulé, P.Z., Covington, W.W., 2004. Plant community variability in ponderosa pine forest has implications for reference conditions. Nat. Area. J. 24, 101–111.

Green, R.H., 1979. Sampling Design and Statistical Methods for Environmental Biologists. Wiley, New York, 257 pp.

Green, R.H., 1993. Application of repeated measures designs in environmental impact and monitoring studies. Aust. J. Ecol. 18, 81–98.

Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. For. Ecol. Manage. 146, 239–245.

Harris, G.R., Covington, W.W., 1983. The effect of prescribed fire on nutrient concentration and standing crop of understory vegetation in ponderosa pine. Can. J. For. Res. 13, 501–507.

Huisinga, K.D., Laughlin, D.C., Fule, P.Z., Springer, J.D., McGlone, C.M., in review. Effects of an intense prescribed fire on ground-flora in a mixed conifer forest. J. Torrey Bot. Soc.

Keane, R.E., Arno, S.F., Brown, J.K., 1990. Simulating cumulative fire effects in ponderosa pine/Douglas-fir forests. Ecology 71, 189–203.

Kerns, B., Moore, M.M., Hart, S.C., 2001. Estimating forest–grassland dynamics using soil phytolith assemblages and $\delta^{13}C$ of soil organic matter. Ecoscience 8, 478–488.

Kilgore, B.M., 1971. The role of fire in managing red fir forests. In: Proceedings of the Transactions of the 36th North American Wildlife and Natural Resource Conference. Wildlife Management Institute, Washington, DC.

Koniak, S., 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Nat. 45, 556–566.

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9, 1179–1188.

Leopold, A., 1941. Wilderness as a land laboratory. Living Wilderness 6, 3.

Mancuso, M., Moseley, R., 1994. Vegetation description, rare plant inventory, and vegetation monitoring for Craig Mountain, Idaho. Unpublished report for the Bonneville Power Administration. On file at: Idaho Department of Fish and Game Conservation Data Center, Boise, Idaho, 146 pp.

Mast, J.N., Fulé, P.Z., Moore, M.M., Covington, W.W., Waltz, A.E.M., 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. Ecol. Appl. 9, 228–239.

Matthews, R.F., 1993. *Delphinium occidentale* and *D. bicolor*. In: Fire Effects Information System [Online]. Fire Sciences Laboratory, US Department of Agriculture, Forest Service, Rocky Mountain Research Station. Available: http://www.fs.fed.us/database/feis/.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, 300 pp.

McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data, version 4. MjM Software Design, Gleneden Beach, Oregon.

McKell, C.M., 1950. A study of plant succession in the oak brush (*Quercus gambelii*) zone after fire. Thesis. University of Utah, Salt Lake City, UT, 79 pp.

Medve, R.J., 1984. The mycorrhizae of pioneer species in disturbed ecosystems of western Pennsylvania. Am. J. Bot. 71, 787–794.

Merriam, C.H., 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. US Department of Agriculture. North American Fauna 3.

Merrill, E.H., Mayland, H.F., Peek, J.M., 1980. Effects of a fall wildfire on herbaceous vegetation on xeric sites in the Selway-Bitterroot Wilderness Idaho. J. Range Manage. 33, 363–367.

Miller, C., 2003. Wildland Fire Use: a wilderness perspective on fuel management. In: Omi, P.N., Joyce, L.A. (Eds.), Fire, Fuel Treatments, and Ecological Restoration. Conference Proceedings RMRS-P-29. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 379–386.

Moore, M.M., Covington, W.W., Fulé, P.Z., 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecol. Appl. 9, 1266–1277.

Moser, E.B., Saxton, A.M., Pezeshki, S.R., 1990. Repeated measures analysis of variance: application to tree research. Can. J. For. Res. 20, 524–535.

Naumburg, E., DeWald, L.E., 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. For. Ecol. Manage. 124, 205–215.

Oswald, B.P., Covington, W.W., 1984. Effect of a prescribed fire on herbage production in southwestern ponderosa pine on sedimentary soils. For. Sci. 30, 22–25.

Pase, C.P., Knipe, O.D., 1977. Effect of winter burning on herbaceous cover on a converted chaparral watershed. J. Range Manage. 30, 346–348.

Poreda, S.F., Wullstein, L.H., 1994. Vegetation recovery following fire in an oakbrush vegetation mosaic. Great Basin Nat. 54, 380–383.

Rabinowitz, D., 1981. Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. Oikos 36, 191–195.

Rasmussen, D.I., 1941. Biotic communities of Kaibab Plateau. Arizona. Ecol. Monogr. 11, 229–275.

Richards, M.S., Landers, R.Q., 1973. Responses of species in Kalsow Prairie, Iowa, to an April fire. Proc. Iowa Acad. Sci. 80, 159–161.

Rusby, H.H., 1889. General floral features of the San Francisco and Mogollon Mts. of Arizona and New Mexico and their adjacent regions. Trans. NY Acad. Sci. 8, 76–81.

Savage, M., 1991. Structural dynamics of a southwestern pine forest under chronic human influence. Ann. Assoc. Am. Geogr. 81, 271–289.

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

Savage, M., Swetnam, T.W., 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71, 2374–2378.

Steel, R.G.D., Torrie, J.H., 1960. Principles and Procedures of Statistics. McGraw-Hill, New York, NY.

Stephenson, N.L., 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. Ecol. Appl. 9, 1253–1265.

Stewart-Oaten, A., Murdoch, W.W., 1986. Environmental impact assessment: "pseudoreplication" in time. Ecology 67, 929–940.

Swetnam, T.W., Baisan, C.H., 1996. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen, C.D. (Ed.), Fire Effects in Southwestern Forests. Proceedings of the Second La Mesa Fire Symposium. USDA Forest Service General Technical Report RM-GTR-286, pp. 11–32.

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

US Department of Agriculture Natural Resource Conservation Service, 2004. The PLANTS database, version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA.

van Mantgem, P., Schwartz, M., Keifer, M., 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Nat. Area. J. 21, 266–273.

Vose, J.M., White, A.S., 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa pine community. For. Ecol. Manage. 40, 175–187.

Warren, P.L., Reichhart, K.L., Mouat, D.A., Brown, B.T., Johnson, R.R., 1982. Vegetation of Grand Canyon National Park. Cooperative National Park Resources Study Unit, Technical Report No. 9.

Woodbury, A., 1944. A history of southern Utah and its National Parks. Utah Historic. Quart. 7, 111–209.

Woolsey, Jr., T.S., 1911. Western yellow pine in Arizona and New Mexico. US Forest Service Bulletin 101. US Government Printing Office, Washington, DC, USA.

Wright, H.A., 1970. A method to determine heat-caused mortality in bunchgrasses. Ecology 51, 582–587.

Wright, H.A., 1971. Why squirrel tail is more tolerant to burning than needle-and-thread. J. Range Manage. 24, 277–284.

Wright, H.A., Klemmedson, J.O., 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology 46, 680–688.

Young, J.A., Evans, R.A., 1978. Population dynamics after wildfires in sagebrush grasslands. J. Range Manage. 31, 283–289.

Young, R.P., Miller, R.F., 1985. Response of *Sitanion hystrix* (Nutt.) J.G. to prescribed burning. Am. Midl. Nat. 113, 182–187.