

# Plant Community Variability in Ponderosa Pine Forest Has Implications for Reference Conditions

**C.N. Gildar**

USDA, Dakota Prairie Grasslands  
McKenzie Ranger District  
1901 S. Main St.  
Watford City, ND 58854 USA  
701-842-2393  
cgildar@fs.fed.us

**P.Z. Fulé<sup>1</sup>**

**W.W. Covington**

Ecological Restoration Institute  
and School of Forestry  
Northern Arizona University  
Box 15018  
Flagstaff AZ 86011 USA

<sup>1</sup> Corresponding author:  
pete.fule@nau.edu; 928-523-1463

**ABSTRACT:** Ponderosa pine plant community and forest structure were compared among three stands in Grand Canyon National Park, Arizona: one stand had 120 years of artificial fire exclusion (NOBURN) and the other two nearby stands had been frequently burned (BURN-E and BURN-W). These forests are valuable places to gauge anthropogenic changes associated with European settlement, due to their land history of limited livestock grazing and no logging. Precipitation varied greatly between sampling years (260 mm in 2000, 505 mm in 2001). Tree density was significantly higher at NOBURN (1424 trees ha<sup>-1</sup>) with significantly higher rotten coarse woody debris (23.2 Mg ha<sup>-1</sup>) and duff depth (4.3 cm) than at the burned sites, as expected in the absence of fire. Although species richness was not significantly different among sites (48-89 species), richness differed significantly by year. Shannon's index of diversity increased by approximately 10% from the dry year to the wet year on all sites. Community composition and plant cover at NOBURN differed significantly from the two burned sites in both years in non-metric multidimensional scaling ordinations. Increasing duff depth was related to decreased plant cover. Two of the three dominant species were different at the fire-excluded site compared to the burned sites. We conclude that although plant community structure was related to fire history, environmental stress and within-stand variability were also important drivers. We suggest selecting reference sites in close proximity to the site to be restored and using a multi-scale, multi-year, multi-site approach to measure reference conditions in ponderosa pine.

*Index terms:* Grand Canyon, Arizona, fire ecology, Kaibab Plateau, ecological restoration

*NOMENCLATURE:* USDA, NRCS. 2002. The PLANTS Database, Version 3.5

## INTRODUCTION

A diverse and productive understory plant community is a vital component of the ponderosa pine forest ecosystem. The understory community contributes virtually all plant biodiversity (since there are usually only 1-4 species of overstory trees), regulates pine regeneration through competition, retains soil, facilitates rapid nutrient turnover rate due to relatively fast decomposition of plant material, and provides wildlife habitat (Rasmussen 1941, Cooper 1960, Naumberg and DeWald 1999, Moore et al. 1999). Understory plants also serve as fuel for frequent surface fires. Fire, being a key disturbance in ponderosa pine forests, has strong influences at the species, community, and ecosystem levels (Cooper 1960, Pearson et al. 1972, Covington and Moore 1994a, 1994b, Moore et al. 1999). In the southwest, the removal of this key disturbance process through livestock grazing, timber harvesting, and fire suppression over the last  $\pm 120$  y resulted in dense forests, reduced understory species composition and plant cover, higher forest floor accumulation, and low nutrient turnover (Arnold 1950, Weaver 1951, Arnold 1953, Cooper 1960, Mitchell and Freeman 1993, Kolb et al. 1994). The increased occurrence of high-intensity crown fires in these densely forested landscapes

may initiate unprecedented ecological trajectories (Moore et al. 1999).

Many researchers and land managers have focused on ecological restoration – “assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Society for Ecological Restoration 2002) – as an adaptive management strategy that not only reduces hazardous fuel loads but treats the underlying causes of declining ecosystem health (Covington 2000, Allen et al. 2002). For example, through the National Fire Plan, the U.S. Department of the Interior allocated over \$102 million toward restoration and rehabilitation of burned lands in fiscal year 2001, including treatment of 911,000 ha to reduce hazardous fuels.

Judgments about ecological degradation and restorative treatments are often based on the range of natural (or “historical”) variability, also known as reference conditions (Landres et al. 1999). Reference information is used to establish restoration goals, determine restoration potential of sites, and evaluate the success of restoration efforts (Jackson et al. 1995, White and Walker 1997, Moore et al. 1999). Aldo Leopold referred to these conditions as a “base datum” for management decisions (1941). Reference conditions are often

poorly understood because of the decay of historical evidence, inherent limitations in the quality and quantity of paleoecological evidence, and changes in climate (Swetnam et al. 1999). Poor information about plant community reference conditions impedes forest restoration planning. For example, Crawford et al. (2001) showed that non-native plants dominated a site severely burned by wildfire on the Kaibab Plateau, Arizona, but they did not have information on the characteristics of the native plant community, making it difficult to assess ecological degradation and recovery except by the crude yardstick of native vs. non-native composition.

Compared to trees, which can live for centuries and decompose slowly, understory plants have short life spans, and most evidence of past plant communities disappears quickly (see Kerns et al. 2001 for an example of persistent grass evidence). A valuable alternative approach is to measure relict areas that are influenced by present-day climatic and other global changes but relatively untouched by the agents of disruption (Thatcher and Hart 1974, Johnson 1986). Unfortunately, relict sites that have not been grazed by domestic livestock and/or logged, and where fires have not been suppressed, are very rare. The few relict areas in southwestern forests tend to be isolated mesas and plateaus often located in National Parks or other protected natural areas (Leopold 1924, Madany and West 1983, Belsky and Blumenthal 1997, Rowlands and Brian 2001, Fulé et al. 2002) or within grazing exclosures (Stohlgren et al. 1999).

To gain a detailed understanding of understory reference conditions on the Kaibab Plateau, we used a multi-scale sampling approach over two growing seasons (2000 and 2001) to measure contemporary structural and functional attributes in remote, relatively undisturbed forests with and without fire exclusion. We sampled two relict "reference sites"—unharvested and frequently burned ponderosa pine forests in Grand Canyon National Park—and compared them to a nearby forest where fire has been excluded since 1879. We sampled more than one reference area (in more than one year) to gauge spatial

and site-specific variation (Anderson and Dugger 1998). We measured the following attributes that might show strong responses to fire exclusion and to forest restoration treatments: forest structure, plant community structure, and above-ground herbaceous biomass (Aronson et al. 1993, Anderson and Dugger 1998). We chose to sample many attributes in a relatively small number of plots, instead of measuring only a few attributes in many plots, to look for relationships among forest structure and plant community. Assessing fire (or fire exclusion) effects often presents statistical difficulties due to pseudoreplication, because study plots are usually nested within a single burned or fire-excluded area (Hurlbert 1984, van Mantgem et al. 2001, Heffner et al. 1996). Carefully matched impacted/reference area studies create useful comparisons between specific burned and unburned sites that limit the role of environmental variability as a causal agent for differences (van Mantgem et al. 2001). Our sites were close in proximity, topography, and elevation and had the same soil type and contemporary vegetation.

We hypothesized that the fire-excluded site would exhibit traits commonly associated with fire exclusion, such as different species composition as well as lower understory species richness, cover, and biomass. We expected that among-site variability between the burned sites and the fire-excluded site would be higher than within-site variability on any site in all responses. Finally, we expected that the two frequently burned sites would be more similar to each other in all measured attributes than to the fire-excluded site.

## METHODS

### Study Area

The three study sites, Powell Plateau, Rainbow Plateau, and Galahad Point, are located in ponderosa pine forests on the Kaibab Plateau, the North Rim of Grand Canyon National Park (Figure 1). This park contains the largest area of never-harvested ponderosa pine forest in Arizona, including 20,000 ha of ponderosa pine (Warren et al. 1982). All three study sites had frequent surface fire regimes until 1879. Weibull

median probability intervals, a measure of fire frequency, ranged from 3.4–3.9 y (all fires) to 6.1–7.5 y (fires scarring  $\geq 25\%$  of sampled trees). No fires had burned at Galahad Point since 1879, the time at which the Kaibab Plateau was affected by land management practices associated with European settlement, such as heavy livestock grazing (Rasmussen 1941, Fulé et al. 2003b). The other sites had several large spreading surface fires and many smaller fires since 1879 (Fulé et al. 2003a). Although the fire regimes are altered at the burned sites, they still represent relatively undisturbed areas (Fulé et al. 2002).

The average elevation and slope of sample plots were 2,314 m elevation and 11% slope on Powell Plateau (BURN-W), 2,308 m, 20.5% slope on Rainbow Plateau (BURN-E), and 2,388 m, 16.3% slope on Galahad Point (NOBURN). Soils are derived from Kaibab Limestone (Bennett 1974). Soils on all sites have been tentatively classified as Elledge Family; well drained, 20–40 inches to bedrock, with about 10 percent gravel (A. Dewall, pers. comm., U.S. Department of Agriculture, NRCS Soil Scientist 2002). Annual precipitation averages 57.9 cm, with an average annual snowfall of 326.9 cm (White and Vankat 1993, GCNP Fire Management Plan 1992). Temperatures measured at the North Rim ranger station ranged from an average July maximum of 26 °C to an average January minimum of -2 °C (Bennett 1974). Precipitation differed in the two years of this study. Grand Canyon weather station records were incomplete, but the Flagstaff weather station (Flagstaff WSO AP at 2137 m elevation) recorded 260 mm total precipitation in 2000 and 505 mm in 2001, representing 47% and 92%, respectively, of the long-term average of 549 mm (Western Regional Climate Center, <www.wrcc.dri.edu>).

Evidence of human occupation of the region dates to 2300 B.P. Native Americans used the highlands for dry farming, hunting, gathering, and gardening (Kelly 1934, Altschul and Fairley 1989). Livestock grazing was initiated by European settlers after 1870. Although grazing was excluded from the park since ~1938, scattered cow dung on BURN-E in 2001 evidenced minimal amounts of recent livestock trespass.

## Forest Structure and Plant Community Sampling

### Plot Selection

A 300 x 300 m sampling grid was established at each study site. A previous study had located 37 permanent plots on BURN-W over 310 ha and 24 plots on BURN-E over 220 ha (Fulé et al. 2002). We selected a subset of six plots on each site for more detailed data collection for the present study. New plots were established on NOBURN in 2000. All plots were purposefully selected from among the grid points using topographic properties as a possible predictor of vegetation attributes (Stohlgren et al. 1999). For each site, two upland flat plots ( $\leq 11\%$  slope), one north-

facing and one south-facing top-slope plot, and one north-facing and one south-facing mid-slope plot were chosen. North-facing plots fell between  $270^\circ$ - $90^\circ$  and south-facing plots fell between  $91^\circ$ - $269^\circ$ . At each plot, we used two sampling techniques overlaid on each other: Modified-Whittaker nested quadrat plots (Stohlgren et al. 1995a) and Ecosystem Monitoring (EM) plots modified from National Park Service fire monitoring protocol (Reeburg 1995, <[www.nps.gov/fire/fmh/FEMHandbook.pdf](http://www.nps.gov/fire/fmh/FEMHandbook.pdf)>). EM plots are effective for measuring forest structure properties, while Modified-Whittaker plots are useful for detailed vegetation information because data is collected at multiple scales. Both types of sampling plots were 0.1 ha (20 x

50 m) in size, oriented with the 50 m sides along an environmental gradient (parallel to the slope in this case).

### Forest Structure

Trees, forest floor and woody debris, and understory vegetation were measured on EM plots in 1998 on BURN-W and BURN-E and in 2000 at NOBURN. Trees larger than 15 cm dbh (diameter at breast height) were measured on the entire 1000 m<sup>2</sup> plot; pole-sized trees (2.5-15 cm dbh) were measured in a 250 m<sup>2</sup> subplot. Seedling trees (< 2.5 cm dbh) were mapped by species, condition, and height in a nested 50 m<sup>2</sup> quadrat. Forest floor depths and fine and coarse woody debris were measured along four 25 m planar transects originating at 10, 20, 30, and 40 m along the center line of each plot and radiating in randomly selected directions. Canopy cover was measured by vertical projection and recorded at 30 cm intervals along the 50 m edges of the EM plots (see Fulé et al. 2002 for detailed methods of EM plots).

### Plant Community

Modified-Whittaker plots were measured at each study site in 2000 and 2001. Nested within each plot were ten 0.5 x 2 m (1-m<sup>2</sup>) subplots; six systematically spaced along the inside border of the 1000-m<sup>2</sup> plot and four systematically arranged along the outside border of the 100-m<sup>2</sup> subplot, two 2 x 5 m (10-m<sup>2</sup>) subplots in alternate corners, and a 5 x 20 m (100-m<sup>2</sup>) subplot in the center (Stohlgren et al. 1998). Foliar cover for each species and substrates were estimated to the nearest one percent in the 1-m<sup>2</sup> subplots (cover of less than one percent was estimated to the nearest 0.25 percent) and cumulative plant species were recorded in the 10-m<sup>2</sup> subplots, the 100-m<sup>2</sup> subplots and the 1000-m<sup>2</sup> plots (Stohlgren et al. 1995b, Stohlgren et al. 1998). Variation in cover and height estimates, due to observer perception on the Modified-Whittaker plots, was minimized by using visual aids for consistency and by standardizing estimates among observers by practice runs before and during data collection.

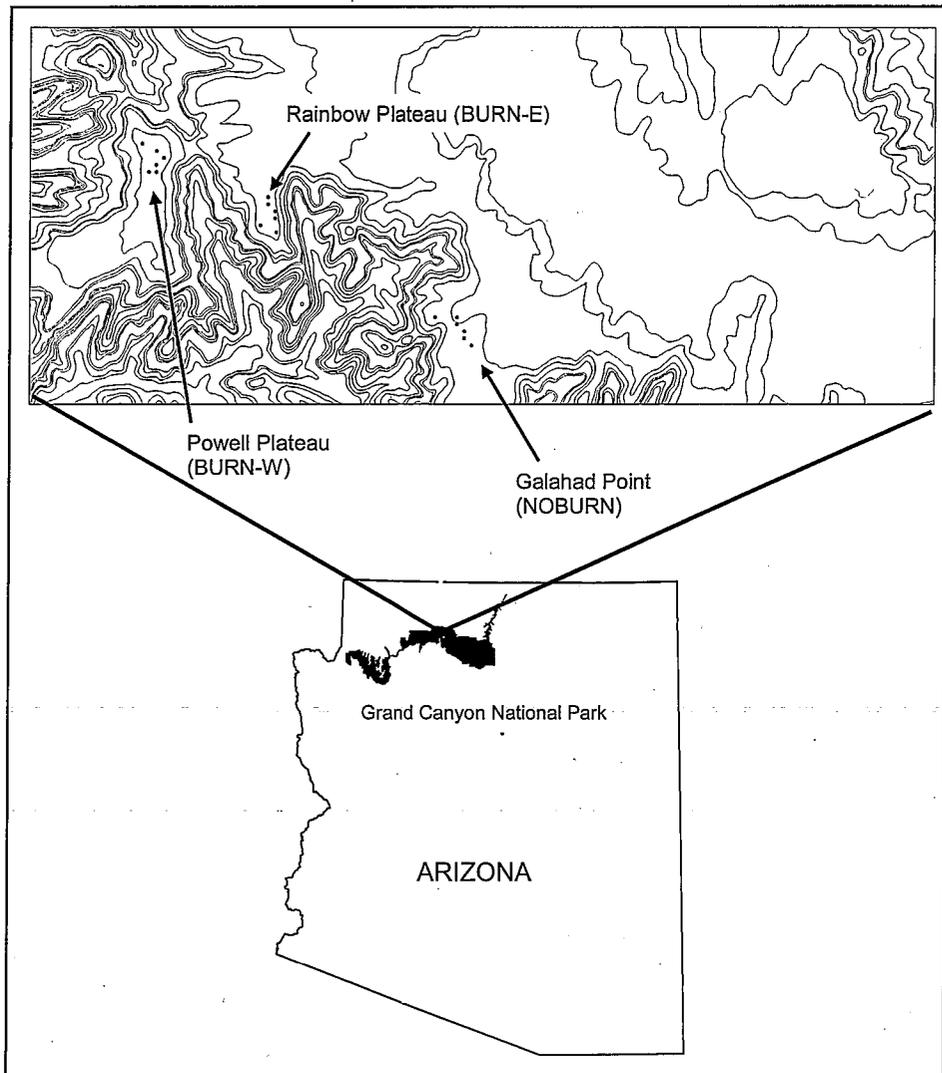


Figure 1. Study area within Grand Canyon National Park, AZ. Plot locations are marked with dark circles.

### Biomass Sampling

Ten 1-m<sup>2</sup> biomass subplots were established along a transect 6 m away from each 50-m side of each vegetation sampling plot. Five random subplots along the transect were clipped in 2000 and the remainder in 2001. Percent foliar cover of each plant species was measured and then all plants in the quadrat were clipped above the root crown and collected by species in paper bags. Only the current year's growth was collected. Dead annual species were collected if they appeared to have grown during the current year. In the case of some perennial herbs, shrubs, and tree seedlings, it was impossible to determine the current year's growth. In those cases, all living plant parts contained within the quadrat were collected. Samples were air dried in the field to prevent molding.

In the lab, clippings were placed in a drying oven at 70 °C to constant weight. Similar studies in this region found 24 h drying time to be sufficient (J.E. Korb, pers. com., 2000).

### Statistical Analyses

We used one-way analyses of variance (ANOVA) to test for differences in the following responses among the three sites: basal area, tree density, regeneration density, percent canopy cover, understory species richness, and herbaceous biomass. Analyses were performed with the SYSTAT 8.0 software (Wilkinson 1988). The alpha level was 0.05. Attributes were transformed when necessary to meet ANOVA assumptions. Arcsine square root transformations were used for attributes with percent values and square root transformations for other attributes. Tukey's Least Significant Difference was used for post-hoc pairwise comparisons. Repeated measures ANOVA was used to test for differences in herbaceous cover in 2000 and 2001. Simple linear regression analyses were performed to determine relationships among forest structure and plant community responses. Regressions were tested for homoskedasticity with residual plots and for leverage of outliers. Kruskal-Wallis analyses were used for attributes with non-normalizable distributions: woody debris and forest

floor depths.

Shannon's index of diversity was calculated using Estimate S software (Colwell 1997) where each sampling plot is added in to calculate an additive index for the site. Estimated understory species richness was calculated using the first order jackknife (JACK) method:

$$JACK = SO + \{r1 (n - 1)\} / n,$$

where SO = the number of species observed in *n* quadrats, and r1 = the number of species present in only one quadrat (Palmer 1990). Jaccard's coefficient (J) calculated species composition overlap among sites. J is defined as:

$$J = A / (A + B + C)$$

where A = the number of species found in both sites, B = species in site 1 but not in site

2, and C = species in site 2 but not in site 1 (Krebs 1989, Stohlgren et al. 1997).

Cover by species by site, and species abundance by site, were ordinated with a non-metric multidimensional scaling method, NMS, in PC-ORD (version 4) (McCune and Mefford 1999). Environmental factors with an  $r^2 \geq 0.5$  were plotted on the ordination graph as "joint plots" (also called "vectors") with the angle and length of the line denoting the direction and strength of the relationship. Statistical significance of difference between sites in ordinations was tested with a multiple permutation procedure using Multi-Response Permutation Procedures in PC-ORD. Species accumulation curves were calculated additively but non-randomly for each site in each year using the EstimateS software (Colwell 1997). The number of new species found in each 1-m<sup>2</sup> subplot on the site was added to the curve consecutively (60

**Table 1. Forest structure of study plots on NOBURN, BURN-E, and BURN-W. Statistics presented are the mean (95% confidence limit), and minimum-maximum. Values within a row that are marked with different letters are significantly different.**

	<i>NOBURN</i>	<i>BURN-E</i>	<i>BURN-W</i>
BA (m <sup>2</sup> ha <sup>-1</sup> )	<b>40.3</b> (7.9) 28.1-50.5	<b>25.5</b> (14.5) 3.0-41.5	<b>34.0</b> (9.3) 25.7-50.8
TPH (trees ha <sup>-1</sup> )	<b>1424.4</b> (1169.1) <b>a</b> 440.2-3440.8	<b>565.2</b> (560.5) <b>b</b> 261.1-1637.1	<b>417.3</b> (343.9) <b>b</b> 90.2-912.9
Canopy Cover (%)	<b>63.8</b> (11.5) 50.8-79.2	<b>45.5</b> (24.4) 9.4-70.6	<b>57.8</b> (13.2) 40.8-77.7

**Table 2. Species composition and abundance of tree regeneration on NOBURN, BURN-E, and BURN-W. Statistics presented are the mean (95% confidence limit), and minimum-maximum.**

<i>Regeneration (seedlings ha<sup>-1</sup>)</i>	<i>NOBURN</i>	<i>BURN-E</i>	<i>BURN-W</i>
Total	<b>7873</b> (11801.5) 200.1-29982.2	<b>4672</b> (5687.2) 0-11942.1	<b>7519</b> (9301.1) 0-23426.3
<i>Pinus ponderosa</i>	<b>169</b> (209.7) 0-413.3	<b>830</b> (1165.5) 0-2772.3	<b>69</b> (177.1) 0-413.3
<i>Quercus gambelii</i>	<b>2822</b> (7252.8) 0-16928.745	<b>1232</b> (3060.6) 0-7182.3	<b>3147</b> (5957.3) 0-14136.5
<i>Robinia neomexicana</i>	<b>4504</b> (5681.7) 0-13053.5	<b>2611</b> (3797.2) 0-9169.8	<b>4302</b> (4827.44) 0-10633.9

subplots total per site), then new species in each 10-m<sup>2</sup> subplot (12 subplots total per site), then all new species found in each 100-m<sup>2</sup> subplot (6 subplots total per site), and finally all new species found in each 1000-m<sup>2</sup> sampling plot (6 total sampling plots per site). Species accumulation curves were also calculated additively and randomly for each site by adding the number of new species found in each 1000-m<sup>2</sup>

sampling plot to a curve.

#### Scope of inference

Relict area studies are generally observational, limiting the scope of inference. Measurements were repeated over time, since we sampled most attributes over two field seasons, but were not spatially replicated. Therefore, we cannot evaluate

how representative our sites are to other forests under similar management and fire regimes. We also cannot rule out site effects as causation for patterns that we found, even when they generally conformed to expectations for burned and unburned sites. Precipitation in 2000 was much lower than in 2001. It would be ideal to sample multiple replicate fire-excluded and burned forests in one area, but we were constrained by the lack of relict sites and the resources available for study in remote sites. Although we cannot extrapolate our findings to other burned and fire excluded areas, we attempted to provide a multi-scale framework and starting point for long-term monitoring of the understory community in these and other reference sites for the southwestern ponderosa pine ecosystem.

## RESULTS

### Study Design

The selection of sampling plots within each study site was planned, using a stratified random design with topographic position, as a potential predictor of vegetation. However, topographic position was not consistently associated with any differences, so variables were compared by site rather than by topographic position.

### Forest Structure

Tree density was significantly higher at NOBURN than at either BURN-W or BURN-E ( $p = 0.04$ ) (Table 1). Basal area and canopy cover were not significantly different among sites. Regeneration of overstory species was not significantly different among sites (Table 2), but species composition and abundance were similar between NOBURN and BURN-W. Both sites had between 7500-8000 total seedlings and sprouts per ha with fewer than 3% ponderosa pine seedlings. On BURN-E, 17% of total regeneration was ponderosa pine seedlings. On all sites, *Robinia neomexicana* Gray (New Mexican locust) sprouts made up approximately 60% of total regeneration. Rotten coarse woody debris (diameter < 7.62 cm) on NOBURN averaged 23.2 Mg ha<sup>-1</sup>, significantly higher than at the burned sites ( $p = 0.004$ ) (Table 3). Duff depth on NOBURN was

**Table 3. Forest floor and woody debris composition on NOBURN, BURN-E, and BURN-W. Statistics presented are the mean (95% confidence limit), and minimum-maximum. Differences were tested with Kruskal-Wallis non-parametric analyses of variance. Values within a row that are marked with different letters are significantly different.**

	NOBURN	BURN-E	BURN-W
Litter depth (cm)	1.3 (0.3) 0-1.8	0.5 (0.3) 0.3-0.762	1.3 (0.8) 0.5-2.03
Duff depth (cm)	4.3 (1.3) a 3.0-5.8	1.5(0.8) b 0.5-2.8	2.5 (0.8) b 1.8-3.8
Fine woody debris (diameter < 7.62 cm), Mg ha <sup>-1</sup>	2.2 (0.8) 1.3-3.1	1.4 (0.8) 0.2-2.0	1.4 (1.0) 0.1-2.4
Sound coarse woody debris (diameter > 7.62 cm), Mg ha <sup>-1</sup>	22.7 (32.5) 0-78.5	3.0 (3.7) 0-9.1	10.6 (18.7) 0-43.6
Rotten coarse woody debris (diameter > 7.62 cm), Mg ha <sup>-1</sup>	23.2 (24.9)a 0.6-23.2	1.6 (3.0)b 0-7.3	0.2 (0.6)b 0-1.5

**Table 4. Observed and estimated species richness and species diversity in 2000 and 2001 on NOBURN, BURN-E, and BURN-W. Statistics presented are the mean (95% confidence limit), and minimum-maximum, except for Shannon's index of diversity, where statistics are presented as the index (standard deviation). Values within a row that are marked with different letters are significantly different.**

	NOBURN	BURN-E	BURN-W
Average Species Richness per plot 2000	21.8 (9.2) 12-32	27.3 (7.3) 20-39	28.2(5.3) 25-38
Average Species Richness per plot 2001	30.0 (11.3) 15-40	37.8 (6.7) 31-47	32.2(7.1) 23-44
Total Species Richness per site 2000 a	48	66	65
Total Species Richness per site 2001 b	61	89	77
Estimated Species Richness 2000 (jackknife)	61.3	86.8	85
Estimated Species Richness 2001 (jackknife)	74.3	115.7	101.2
Shannon's Index of diversity 2000	3.26 (0.04)	3.52 (0.06)	3.49 (0.05)
Shannon's Index of diversity 2001	3.63 (0.03)	3.83 (0.04)	3.75 (0.05)

significantly higher than the burned sites ( $p = 0.002$ ) (Table 3). Fine woody debris and litter depths were not significantly different among sites.

### Species Richness and Composition

Species richness was not significantly different among sites in either year, but richness within sites differed significantly from 2000 (less precipitation) to 2001 (more precipitation) ( $p < 0.0001$ ). Species richness increased from 48 to 61 on NOBURN, 65 to 77 on BURN-W, and 66 to 89 on BURN-E. A previous study that measured plots over more area on BURN-W and BURN-E found the species pool to be approximately 110 species for each site (J.D. Springer, unpublished data).

Species richness was not well correlated with herbaceous cover or herbaceous biomass (data below). In both years, observed species richness was between 76-82% of estimated species richness on all sites (Table 4). Pairwise comparisons of species overlap between sites (Jaccard's coefficient) ranged from 44%-53% in both years (Table 5). Species with less than 1% average cover comprised at least 65% of total species composition on each site. While values were relatively constant between years on the burned sites, the number of species with less than 1% cover decreased from 90% to 77% on NOBURN in 2001, the year with higher precipitation.

Shannon's index of diversity ( $H'$ ) was lowest on the fire-excluded site in both years (3.26 in 2000 and 3.63 in 2001). On all sites,  $H'$  increased by approximately 10% from the dry year (2000) to the wet year (2001). Shapes of species accumulation curves from the 1-m<sup>2</sup> to 1000-m<sup>2</sup> scale were different on BURN-W than on BURN-E and NOBURN in 2000. The curve for BURN-W leveled out with a greater number of samples, while BURN-E and NOBURN were still increasing. But in 2001, curves for all sites appeared to have similar shapes, and there was complete overlap between BURN-E and BURN-W (Figure 2). Species accumulation curves generated only from the 1000-m<sup>2</sup> scale data did not level off for any site on either year.

Table 5. Pairwise comparisons of species overlap between sites calculated by Jaccard's coefficient of similarity for NOBURN, BURN-E, and BURN-W.

Jaccard's coefficient of similarity (year)	NOBURN / BURN-E	NOBURN / BURN-W	BURN-E / BURN-W
2000	0.443	0.42	0.489
2001	0.505	0.442	0.533

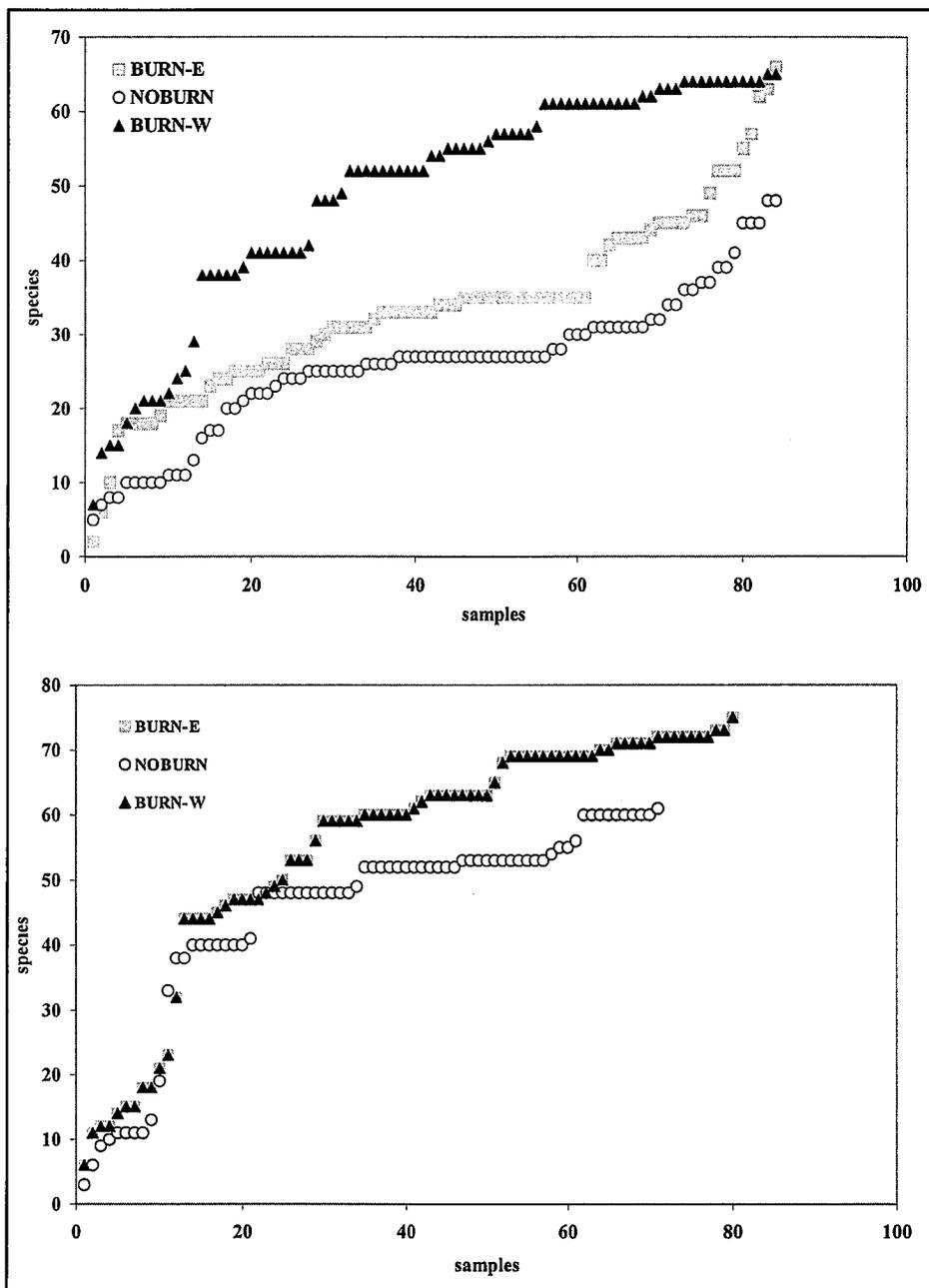


Figure 2. Species accumulation curves for BURN-E, NOBURN, and BURN-W in 2000 (top) and 2001 (bottom). Species accumulation curves were calculated additively but non-randomly for each site in each year using the EstimateS software (Colwell 1997).

**Table 6. Herbaceous cover and biomass in 2000 and 2001 on NOBURN, BURN-E, and BURN-W. Statistics presented are the mean (95% confidence limit), and minimum-maximum. Values within a row marked with different letters are significantly different.**

	<i>NOBURN</i>	<i>BURN-E</i>	<i>BURN-W</i>
Herbaceous Cover (%) 2000	1.3 (0.6) a 0.7-2.3	6.2 (3.6) b 3.6-12.8	5.8 (4.4) 1.5-11.6
Herbaceous Cover (%) 2001	2.1 (0.10) a 0.8-3.1	8.4 (2.9) 5.3-12.6	10.4 (7.5) b 1.6-19.3
Forb Cover (%) 2000	0.5 (0.5)	3.3 (2.1)	3.9 (3.5)
Forb Cover (%) 2001	0.9 (1.0)	5.5 (3.3)	8.5 (7.4)
Graminoid Cover (%) 2000	0.8 (0.3)	2.9 (2.3)	1.6 (0.9)
Graminoid Cover (%) 2001	1.2 (0.5)	2.6 (0.8)	1.6 (1.1)
Annual Cover (%) 2000	0	0	0.3 (0.6)
Annual Cover (%) 2001	0	0.3 (0.3)	0.3 (0.7)
Herbaceous + Subshrub biomass 2000 (kg/ha)	48.512 (44.843) 6.928-125.728	174.535 (134.3) 60.8-402.6	90.6 (28.6) 59.8-129.3
Herbaceous + Subshrub biomass 2001 (kg/ha)	126.390 (100.783) 43.542-297.615	156.1 (145.5) 8.1-402.5	256.7 (275.8) 20.2-717.2
Herbaceous biomass 2000 (kg/ha)	42.9 (44.9) a 6.6-122.9	171.0 (136.5) b 59.3-402.6	82.02 (46.72) 34.22-158.1
Herbaceous biomass 2001 (kg/ha)	126.4 (100.8) 43.5-297.6	156.1 (145.5) 8.1-402.5	198.2 (165.72) 202.1-394.1
Forb biomass 2000 (kg/ha)	19.6 (33.2)	64.3 (76.0)	36.8 (39.9)
Forb biomass 2001 (kg/ha)	87.6 (112.6)	57.1 (81.8)	159.0(142.8)
Graminoid biomass 2000 (kg/ha)	25.7 (16.3)	106.7 (68.8)	38.1 (14.8)
Graminoid biomass 2001 (kg/ha)	33.9 (29.4)	85.7 (166.1)	38.2 (61.7)
Annual biomass 2000 (kg/ha)	0.0	0	4.8 (12.3)
Annual biomass 2001(kg/ha)	4.8 (10.1)	12.5 (17.4)	1.1 (0.9)

Percentage of species that appeared and disappeared from a site between the two sampling years differed the most between NOBURN and BURN-W. On NOBURN, 72% of the species were present in both years, while on BURN-W only 61% were common between the two years. The number of annuals that appeared on each site was similar between both sites (4-5 species). On BURN-E, seven new annual species appeared in 2001. Forbs were the

most common growth form to appear to any site.

Composition of dominant species was different among sites. *Poa fendleriana* (Steud.) Vasey (Poaceae) was the most frequently encountered species on both burned sites in both years, followed by *Elymus elymoides* (Raf.) Swezey (Poaceae) and *Eriogonum racemosum* Nutt. (Polygonaceae). Other dominant species differed between burned

sites. *Carex geophila* Mack. (Cyperaceae) was the most commonly occurring species on NOBURN, followed by *Poa fendleriana* (Steud.) Vasey, *Mahonia repens* (Lindl.) G. Don, *Robinia neomexicana* Gray, and *Carex rossii* Boott (Cyperaceae).

Legumes and grasses were among the most frequently found plant functional groups on all sites in both years. On all sites, one legume species was clearly dominant over all other legumes, but a different species was most common on each site. In both years, *Robinia neomexicana* Gray, a tree species, was most common on NOBURN. Herbaceous legume species were most common on both burned sites: *Lotus utahensis* Ottley (Fabaceae) on BURN-E and *Lupinus hillii* Greene on BURN-W. Several species of cool season (C3 pathway) grasses were found on all sites, with *Poa fendleriana* (Steud.) Vasey clearly the dominant species.

No exotic species were found on NOBURN. *Bromus tectorum* Greene (cheat-grass, Poaceae) was present on BURN-W in both years and on BURN-E in 2001. Casual observations suggested that hikers spread *B. tectorum* Greene on BURN-W, since it was found almost exclusively near the established trail and along a commonly traveled cross-country route. *Tragopogon dubius* L. (yellow salsify, Asteraceae) was found at both burned sites in trace amounts. *Taraxacum officinale* G.H. Weber ex Wiggers (common dandelion, Asteraceae) was found on BURN-E in trace amounts.

A related study (C. Gildar and S. Powers, unpubl.) found that the buried viable seed bank of all sites was depauperate relative to the above-ground plant community. Similarity between above- and below-ground species composition was low: coefficient of community ranged from 17-26%. Species richness was made up largely of perennial forbs, but composition differed among all sites. Significantly more seeds germinated from the forest floor layer of NOBURN than from the burned sites ( $p = 0.021$ ).

#### Herbaceous cover

Total herbaceous cover was significantly

lower on NOBURN than BURN-E in 2000 ( $p = 0.04$ ) and BURN-W in 2001 ( $p = 0.02$ ) (Table 6). There was a significant effect of year on herbaceous cover ( $p = 0.04$ ). When separated into growth forms, forb cover was at least five times greater on the burned sites than on NOBURN in both years. On the burned sites, there was a trend toward the proportion of total cover made up by forb species (increasing in 2001).

Nonmetric multidimensional scaling ordinations of herbaceous cover by species (Figure 3) showed that NOBURN separated from the two burned sites in both years, but that the burned sites were interspersed. This separation was clearer in 2000. In both years, joint plots (also called vectors) showed that increasing duff depth was associated with decreased plant cover (Figure 3). Multi-response permutation procedures analysis showed that there were significant differences among sites: herbaceous cover 2000 ( $p < 0.0001$ ,  $A = 0.271$ ); herbaceous cover 2001 ( $p < 0.0001$ ,  $A = 0.300$ ). Ordination based on abundance of individuals, rather than cover, gave similar results: significant separation of the NOBURN plant community and an increasing duff depth vector associated with NOBURN (data not shown).

### Herbaceous biomass

Total herbaceous biomass was significantly lower at NOBURN than at BURN-E in 2000 ( $p = 0.04$ ), but there was no significant biomass difference among sites in 2001 (Table 6). However, at all sites, herbaceous biomass varied greatly among plots. Biomass differed significantly between 2000 and 2001 ( $p = 0.046$ ). Forb biomass followed the same trend as forb cover; this growth form showed the largest increase between years and also made up a greater proportion of total biomass in 2001.

## DISCUSSION

### Forest Structure

Tree density, forest floor, and coarse woody debris were significantly higher at NOBURN (Tables 3 and 5), conforming to typical conditions in a fire-excluded ponderosa pine forest (Covington and Moore

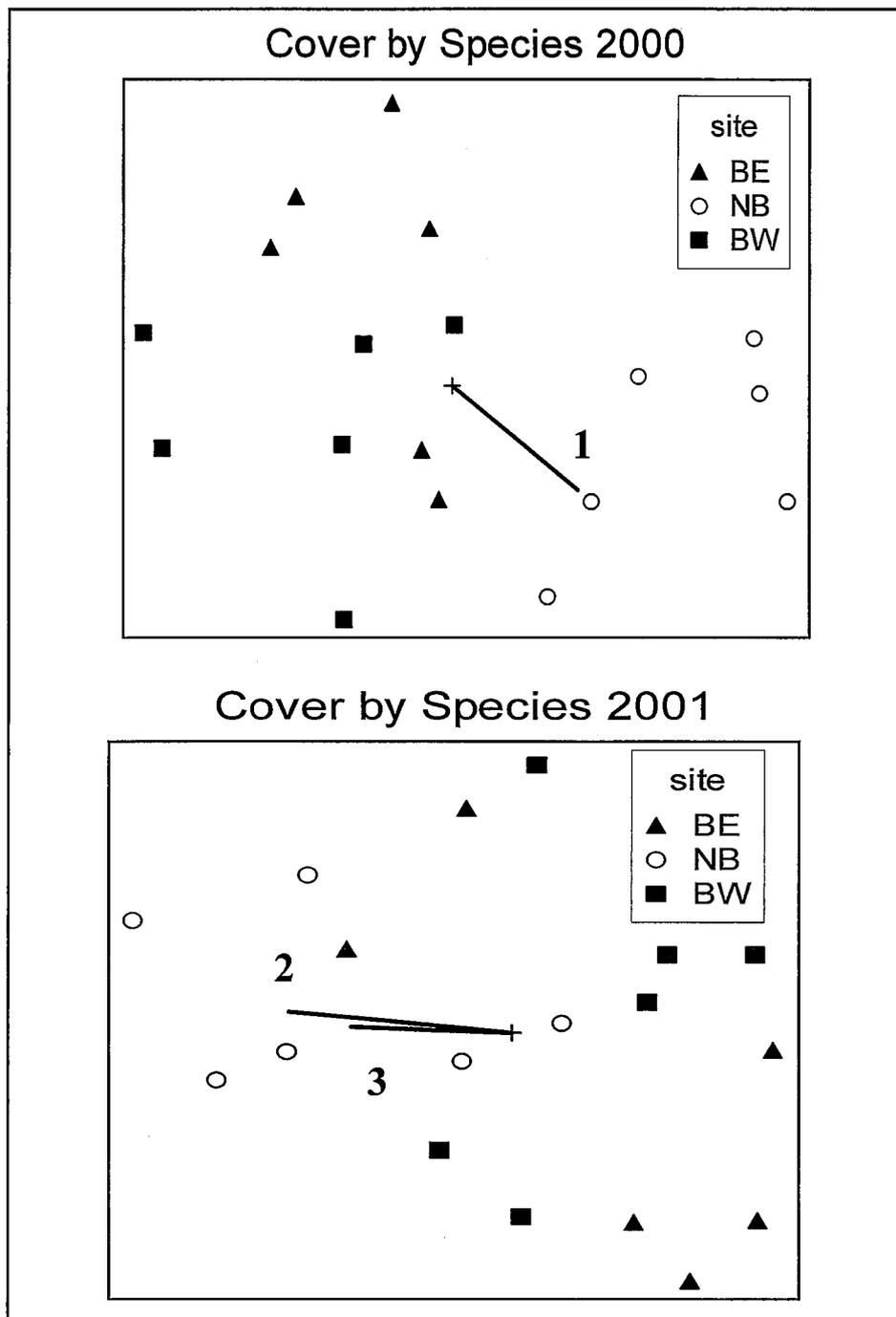


Figure 3. Ordinations of species cover by site in 2000 and 2001 on NOBURN (NB), BURN-E (BE), and BURN-W (BW). Vectors show direction and strength of relationship between plant cover and environmental attributes. 1 = duff depth ( $r^2=0.39$ ), 2 = duff depth ( $r^2=0.70$ ), 3 = rotten coarse woody debris ( $r^2=0.51$ ).

1994b). Live trees, woody, and forest floor debris all hold nutrients, so higher levels of this living and undecayed matter on NOBURN suggest that nutrient storage may be higher there than at the burned sites. Covington and Sackett (1984) found that rotten coarse woody debris had the highest

nutrient content for N, Ca, Mg, and K (in  $g/m^2$ ) and decreased disproportionately compared to sound woody debris after a prescribed fire in northern Arizona.

The finding that higher forest floor accumulation at NOBURN was related to

diminished herbaceous cover and species abundance in our study (Figure 3) is consistent with a meta-analysis of 35 independent studies world-wide showing overall negative effect of plant litter on vegetation (Xiong and Nilsson 1999). They showed that species richness was more affected by plant litter than above-ground biomass, and seedling germination was more affected than seedling establishment, suggesting that inter-specific competition may be influenced by litter layers (Xiong and Nilsson 1999). Our findings are consistent since species richness was lowest at NOBURN, though the difference was not statistically significant, and species richness of the seed bank and number of germinated seeds was highest at NOBURN. Forest floor material in the field may have prevented seeds from germinating and, therefore, allowed them to stockpile in the soil seed bank, but disturbance of that layer and greenhouse conditions may have been appropriate cues for germination.

Overstory regeneration was more similar between NOBURN and BURN-W in quantity and composition than between the two burned sites (Table 2), failing to support our hypothesis that the two burned sites would be more similar to each other than to NOBURN. Most surprising was the high abundance of pine seedlings on BURN-E, especially since this site had much higher herbaceous cover to hinder seedling establishment when compared to NOBURN.

### Plant Community

We expected to find differences in plant community responses between NOBURN and the burned sites, but did not expect to find these differences between burned sites. However, species richness, herbaceous cover, and herbaceous biomass were temporally variable within sites and spatially variable within each year between burned sites (Tables 4 and 6). Had we only sampled one year, or one burned site, we would have failed to detect between 15-27 species and differing patterns of variability between the burned sites. Detecting variability is important not only because it adds to our understanding of the range of variability within ponderosa pine forests, but also

because this variability contributes to overall landscape heterogeneity. For example, along a Canadian Arctic river, degree of differentiation among stands ( $\beta$ -diversity, measured by Jaccard's coefficient in our study) was a more important contributor to the species richness over the landscape ( $\gamma$ -diversity) than species richness within a stand ( $\alpha$ -diversity) (Gould and Walker 1999).

Species accumulation curves (Figure 2) of all three sites show varied site responses between years and variation in response among sites within a year. NOBURN had the least amount of species in both years. Although burned sites had similar number of species, they were distributed differently on the landscape in the dry year. On BURN-W, the curve leveled out after approximately 60 samples, or all the 1-m<sup>2</sup> subplots, and 94% of species were found in those small subplots. Therefore, species were relatively evenly distributed on the landscape. BURN-E's curve, however, increased after approximately 60 samples, and only 53% of species were found in the 1-m<sup>2</sup> subplots. The species found only in the larger subplots are rarer and more patchily distributed, since they were detected after many more sampling plots were added. Both BURN-E and NOBURN exhibited this pattern in the dry year, and changed patterns to level out at the end of their curves in the wet year. BURN-W appeared to be resistant to short-term climatic fluctuation, while the change in the shape of the curves on BURN-E and NOBURN suggest that these sites may have been resilient to fluctuation. Species accumulation curves using only 1000 m<sup>2</sup> scale data did not level off for any site in either year, indicating that our sample size did not capture the majority of species on any site.

The below-ground species pool on NOBURN, BURN-E, and BURN-W was found to be low in a related study (C. Gildar and S. Powers, unpubl.), suggesting that the buried viable soil seed bank on these sites may not be the major source of new propagules (see also Vose and White 1987). Therefore, assessing and monitoring the effectiveness of the other vehicles of natural regeneration, such as seed dispersal from

nearby areas and vegetative reproduction, would be appropriate in conjunction with any restoration treatments at NOBURN.

Ordination analysis showed that the plant community at the fire-excluded site was significantly different from the burned sites in both years in a multivariate sense, but many individual attributes examined in this study showed large within-site and between-year variability, as evidenced in the data by large ranges of response and wide confidence intervals of mean responses. Within-site variability had no consistent pattern; i.e., overall, NOBURN did not tend to be more or less variable than the burned sites. Attributes on the burned sites had different responses between years when compared to NOBURN and to each other.

Within the same year, burned sites differed from each other in herbaceous biomass, overstory species seedling composition, forest floor depths, species richness, and species composition. BURN-E and BURN-W may be some of the best examples of contemporary reference sites available for southwestern ponderosa pine (Fulé et al. 2002). The high variability between these closely matched sites is a strong argument for carefully assessing range of natural variability in forest restoration and ecosystem management. Furthermore, there are twelve habitat types of ponderosa pine forests and seven phases within those types in southern Arizona and portions of the Colorado Plateau (Muldavin et al. 1996). These types have different dominant understory species, and some types have a more prominent shrub component. It could be a harmful oversimplification to assume that what is represented in one relatively intact site is the definitive blueprint for other degraded sites in this ecosystem.

### MANAGEMENT IMPLICATIONS

Recent fire seasons continue to increase in severity. In 2000, almost 567,000 ha burned in the United States, exceeding the 10-year average by over 80,000 ha. Fire activity in 2002 far outpaced the average, with 2.8 million ha burned (National Incident Information Center 2003). As restoration research continues and prescriptions are

implemented and monitored, adaptive management strategies that incorporate new findings can be used to increase effectiveness of restoring ecosystem health to ponderosa pine systems. Our study suggests that plant communities in relatively undisturbed areas respond to environmental stress and small-scale variation as well as to fire suppression.

Although several ecosystem attributes in this study did correspond to fire history, including higher forest density, lower species richness, and deeper forest floor at the NOBURN site, we suggest that it is not appropriate to extrapolate reference information to distant ponderosa pine forests. Reference information from BURN-W and BURN-E could guide potential restoration treatments on NOBURN, forests on the North Rim of Grand Canyon National Park and North Kaibab Ranger District, and perhaps other forests within the same habitat type. However, a 'one-size-fits-all' prescription to guide treatments for northern Arizona forests would be inappropriate because it would not take into account differences in pre-settlement conditions throughout the region. We suggest using a multi-scale approach to assess scales of variability of ecosystem attributes in ponderosa pine ecosystems. In addition, sampling for several years and at more than one relict site will allow future studies to incorporate the effects of spatial heterogeneity and short-term climatic variability versus the "snapshot-in-time" of shorter studies.

#### ACKNOWLEDGMENTS

This project was funded by the Ecological Restoration Institute. Bradford Blake provided greenhouse support. Bob Winfree, Della Snyder, and Melissa Schroeder of Grand Canyon National Park provided logistical support. Tom Stohlgren made valuable comments on a draft of this manuscript. Kambria Beck, Julie Blake, Walker Chancellor, Mark Daniels, Rebecca deGroot, Emery Edwards, Marta Fisher, Sommer Flower, Amber Hughes, Gina Henry, Kristin Huisinga, Lauren Labate, Julia Mack, Chris McGlone, Andrea Meronuck, Daniel Murray, Stephanie Powers, Sarah Quinn, Michael Tweiten, Brent

Tyc, Melanie Walker, and Diane Welles provided enthusiastic field support.

---

*Cara Gildar is a botanist with the U.S. Forest Service, Dakota Prairie Grasslands. She is interested in assessing the roles disturbance plays in forest and grasslands plant communities and in using reference information as a tool for natural resource management planning.*

*Pete Fulé and Wally Covington are faculty members at Northern Arizona University with research interests in fire ecology and forest restoration.*

#### LITERATURE CITED

- Allen, C.D., D.A. Falk, M. Hoffman, J. Klingel, P. Morgan, M. Savage, T. Schulke, P. Stacey, K. Suckling, and T.W. Swetnam. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad framework. *Ecological Applications* 12:1418-1433.
- Altschul, J.H., and H.C. Fairley. 1989. Man, models, and management: an overview of the archaeology of the Arizona strip and the management of its cultural resources. Prepared for: U.S. Department of Agriculture, Forest Service and U.S. Department of the Interior, Bureau of Land Management (Contract No. 53-8371-6-0054), Statistical Research, Plateau Archaeology, Dames & Moore, Inc. 410 pp.
- Anderson, D.H., and B.D. Dugger. 1998. A conceptual basis for evaluating restoration success. *Trans. North American Wildlife and Natural Resource Conference* 63:111-121.
- Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in Northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry* 48:118-126.
- Arnold, J.F. 1953. Effect of heavy selection logging on the herbaceous vegetation in a ponderosa pine forest in Northern Arizona. *Journal of Forestry* 52:101-105.
- Aronson, J., C. Floret, E. LeFloc'h, C. Ovalle, and R. Pontanier. 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A view from the South. *Restoration Ecology* 1:8-17.
- Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. *Conservation Biology* 11:315-327.
- Bennett, P.S. 1974. The fire ecology of the ponderosa pine ecosystem of the North Rim forests, Grand Canyon National Park.

- Report on file at Grand Canyon National Park, Ariz. 136 pp.
- Colwell, R.K. 1997. Estimate S. Users Guide and application. Available online <www.viceroy.eeb.uconn.edu/estimates>.
- Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern ponderosa pine forests since white settlement. *Ecological Monographs* 30:129-164.
- Covington, W.W. 2000. Helping western forests heal. *Nature* 408:135-136.
- Covington, W.W., and M.M. Moore. 1994a. Southwestern ponderosa forest structure --changes since Euro-American settlement. *Journal of Forestry* 92:39-47.
- Covington, W.W., and M.M. Moore. 1994b. Postsettlement changes in natural fire regimes: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153-181.
- Covington, W.W., and S.S. Sacket. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science* 30:183-192.
- Crawford, J.A., C.H.A. Wahren, S. Kyle, and W.H. Moir. 2001. Responses of exotic plant species to fires in Pinus ponderosa forests in northern Arizona. *Journal of Vegetation Science* 12:261-268.
- Fulé, P.Z., W.W. Covington, M.M. Moore, T.A. Heinlein, and A.E.M. Waltz. 2002. Natural variability in forests of Grand Canyon, USA. *Journal of Biogeography* 29:31-47.
- Fulé, P.Z., T.A., Heinlein, W.W. Covington, and M.M. Moore. 2003a. Assessing Grand Canyon fire regimes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12:(2):129-145.
- Fulé, P.Z., J.E. Crouse, T.A. Heinlein, M.M. Moore, W.W. Covington, and G. Verkamp. 2003b. Mixed-severity fire regime in a high-elevation forest: Grand Canyon, Arizona. *Landscape Ecology* 18:465-486.
- GCNP [Grand Canyon National Park] 1992. Fire Management Plan. On file at Grand Canyon National Park, Ariz. 223 pp.
- Gould, W.A., and M.D. Walker. 1999. Plant communities and landscape diversity along a Canadian Arctic river. *Journal of Vegetation Science* 10:537-548.
- Heffner, R.A., M.J. Butler IV, and C.K. Reilly. 1996. Pseudoreplication revisited. *Ecology* 77:2558-2562.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2):187-211.
- Jackson, L.L., N. Lopoukhine, and D. Hillyard. 1995. Commentary ecological restoration: a definition and comments. *Restoration Ecol-*

- ogy 3(2):71-75.
- Johnson, D.W. 1986. Desert buttes: natural experiments for testing theories of island biogeography. *National Geographic Research* 2:152-166.
- Kelly, I.T. 1934. Southern Paiute bands. *American Anthropologist* 36:548-560.
- Kerns, B.K., M.M. Moore, and S.C. Hart. 2001. Estimating forest-grassland dynamics using soil phytolith assemblages and "delta"<sup>13</sup>C of soil organic matter. *EcoScience* 8: 478-488.
- Kolb, T.E., M.R. Wagner, and W.W. Covington. 1994. Concepts of forest health: utilitarian and ecosystem perspectives. *Journal of Forestry* 92:10-15.
- Krebs, C.J. 1989. *Ecological Methodology*. Harper & Row, New York. 654 pp.
- Landres, P.B., P. Morgan, and J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:117-1188.
- Leopold, A. 1924. Grass, brush, timber, and fire in southern Arizona. *Journal of Forestry* 22:1-10.
- Leopold, A. 1941. Wilderness as a land laboratory. *Living Wilderness* 6:3.
- Madany, M.H., and N.E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64:661-667.
- McCune, B., and M.J. Mefford. 1999. PC-ORD. MjM Software Design, Gleneden Beach, Oregon, USA.
- Mitchell, J.E., and D.R. Freeman. 1993. Wildlife-livestock-fire interactions on the North Kaibab: a historical review. U.S. Department of Agriculture, Forest Service, General Technical Report, GTR-RM-222, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 12 pp.
- 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.
- Muldavin, E.H., R.L. DeVelice, and F.L. Ronco. 1996. A Classification of Forest Habitat Types Southern Arizona and Portions of the Colorado Plateau. General Technical Report RM-GTR-287. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 130 pp.
- National Incident Information Center. Wildland fire statistics (accessed June 24, 2003). Available online <<http://www.nifc.gov/fire-info/2002/index.html>>.
- 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.
- Palmer, M.W. 1990. The estimation of species richness by extrapolation. *Ecology* 71:1195-1198.
- Pearson, H.A., J.R. Davis, and G.H. Schubert. 1972. Effects of wildfire on timber and forage production in Arizona. *Journal of Range Management* 25:250-253.
- Rasmussen, D.I. 1941. Biotic communities of Kaibab Plateau, Arizona. *Ecological Monographs* 11:229-276.
- Reeburg, P. 1995. The western region fire monitoring handbook. Pp. 259-260 in U.S. Department of Agriculture, Forest Service General Technical Report INT-GTR-320. Intermountain Forest and Range Experiment Station, Ogden, Utah. 283 pp.
- Rowlands, P.G., and N.J. Brian. 2001. Fishtail mesa: a vegetation resurvey of a relict area in Grand Canyon National Park, Arizona. *Western North American Naturalist* 61:159-181.
- Society for Ecological Restoration. 2002. SER primer on ecological restoration. Available online <<http://www.ser.org>>.
- Stohlgren, T.J., M.B. Falkner, and L.D. Schell. 1995a. A Modified-Whittaker nested vegetation sampling method. *Vegetatio* 117:113-121.
- Stohlgren, T.J., D. Binkley, T.T. Veblen, and W.L. Baker. 1995b. Attributes of reliable long-term landscape-scale studies: malpractice insurance for landscape ecologists. *Environmental Monitoring and Assessment* 36:1-25.
- Stohlgren, T.J., M.B. Coughenour, G.W. Chong, D. Binkley, M.A. Kalkhan, L.D. Schell, D.J. Buckley, and J.K. Berry. 1997. Landscape analysis of plant diversity. *Landscape Ecology* 12:155-170.
- Stohlgren, T.J., K.A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management* 51:164-172.
- Stohlgren, T.J., L.D. Schell, and B.V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* 9:45-64.
- Swetnam, T.W., C.D. Allen, and J.L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189-1206.
- Thatcher, A.P., and V.L. Hart. 1974. Spy Mesa yields better understanding of pinyon-juniper in range ecosystem. *Journal of Range Management* 27:354-357.
- van Mantgem, P., M. Schwartz, and M. Keifer. 2001. Monitoring fire effects for managed fires and wildfires: coming to terms with pseudoreplication. *Natural Areas Journal* 21:266-273.
- Vose, J.M., and A.S. White. 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. *Canadian Journal of Botany* 65:2280-2290.
- Warren, P.L., K.L. Reichhart, D.A. Mouat, B.T. Brown, and R.R. Johnson. 1982. Vegetation of Grand Canyon National Park. Cooperative National Park Resources Study Unit, Technical Report No. 9. 140 pp.
- Weaver, H. 1951. Observed effects of prescribed burning on perennial grasses in the ponderosa pine forests. *Journal of Forestry* 49:267-271.
- White, M.A., and J.L. Vankat. 1993. Middle and high elevation coniferous forest communities of the North Rim region of Grand Canyon National Park, Arizona, USA. *Vegetatio* 109:161-174.
- 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.
- Wilkinson, L. 1988. SYSTAT. Evanston, Illinois, USA.
- Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* 87:984-994.