Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 235 (2006) 283–294
Forest Ecology and Management
www.elsevier.com/locate/foreco

Changes in understory vegetation of a ponderosa pine forest in northern Arizona 30 years after a wildfire

Amanda L. Bataineh [a,*], Brian P. Oswald [a], Mohammad M. Bataineh [b], Hans M. Williams [a], Dean W. Coble [a]

[a] *Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, P.O. Box 6109, SFA Station, Nacogdoches, TX 75962, United States*
[b] *Department of Natural Resources and Environment, Jordan University of Science and Technology, P.O. Box 3030, Irbid 22110, Jordan*

Received 3 October 2005; received in revised form 1 September 2006; accepted 3 September 2006

Abstract

Wildland fires can cause shifts in understory species composition and production. Many studies have examined short-term changes in understory vegetation following a wildfire; however, very few long-term studies are available. The objective of this study was to examine changes in understory (herbaceous and shrub) species composition and production since the 1972 Rattle Burn wildfire on the Coconino National Forest near Flagstaff, Arizona. Understory species composition and production were originally sampled in 1972, 1974, and 1980 and were re-sampled during July and August of 2002 and 2003 on 30 plots in each of four sites: high severity burn, low severity burn, unburned site prescribed burned in 1977, and an unburned site. Repeated measures analysis was used to test for the effects of fire and time on understory species production. The effects of fire on understory species composition were tested using multi-response permutation procedures (MRPP). A lingering effect of the Rattle Burn wildfire on the understory plant production and composition was revealed. Severely burned sites, which had the least pine basal area, may have greater understory production as compared to unburned sites up to 30 years after a wildfire. However, species composition on all sites was altered. A significant, negative relationship was found between tree basal area and understory species composition and production for 1972 and 2003.

Keywords: Understory vegetation; Wildfire; *Pinus ponderosa*; Succession; Coconino National Forest

1. Introduction

Historically, the natural fire return interval in Arizona ponderosa pine (*Pinus ponderosa* P. and C. Lawson) communities ranged from <5 to 17 years (Dieterich, 1980; Fulé et al., 1997). This short fire return interval maintained an open forest with an herbaceous understory (Wright and Bailey, 1982; Covington and Moore, 1994). However, fire frequency has decreased since European settlement due to landscape level fuel fragmentation from roads, decreased herbaceous fuels from livestock grazing, fire suppression, and timber management activities (Cooper, 1960; Mast et al., 1999). This decrease in fire frequency has resulted in a decrease in herb and shrub productivity (Covington and Moore, 1994), and is commonly associated with an increase in tree density (Moore and Deiter, 1992; Naumberg et al., 2001; Moore et al., 2004), crown closure, and litter depth (Clary et al., 1968).

Fire alters understory species composition and production by removing non-resistant plants, pine needles, and woody debris; which in turn, temporarily increases nutrient availability, provides bare mineral soil that is conducive for colonization, and reduces competition for moisture and light (Wright and Bailey, 1982; Pyne et al., 1996). The remaining individuals may utilize the nutrients released and increase their growth rates (Goodwin and Sheley, 2001). Thus, post-fire communities are composed of fire-resistant plants and plant species from adjacent communities that are able to establish, grow, and regenerate, thereby providing seeds for colonization of nearby sites. However, the degree of change from pre-fire community to post-fire community is influenced by the intensity, severity, periodicity, and seasonality of the fire (Wright and Bailey, 1982), as well as other factors like precipitation cycles (Anderson et al., 1968; Moore et al., 2006) and grazing patterns (Krueger and Winward, 1974; Madany and West, 1983; Zimmerman and Neuenschwander, 1984).

---

* Corresponding author. Tel.: +1 936 468 1184; fax: +1 936 468 2489.
E-mail address: rountree_amanda@hotmail.com (A.L. Bataineh).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.09.003

A number of studies have examined short-term changes in understory vegetation following fire in ponderosa pine stands of northern Arizona and New Mexico. Pearson et al. (1972) reported an increase in understory plant production the first year after a wildfire in moderately and severely burned areas compared to an unburned area. Ffolliott et al. (1977) reported an increase in herbage production for up to 11 years after a prescribed burn compared to an unburned area. Lowe et al. (1978) reported a peak in forb production 3 years after a fire. However, forbs production did not differ from an unburned area 7 years after the fire. Grass production declined the first year after the fire, peaked at year 7, and remained twice the production of an unburned area at year 20 (Lowe et al., 1978). Foxx (1994) reported that sites where the overstory was removed by a wildfire produced a linear increase in total understory production for at least 16 years; whereas, sites where the overstory remained intact after the wildfire, total understory production decreased for the first 2 years but increased later. Both, Crawford et al. (2001) and Griffis et al. (2001) reported increased species richness and abundance of exotic plant species within 5 years on wildfires that killed 90% or more of the trees, compared to both moderately burned sites and thinned and burned sites. Laughlin et al. (2004) reported an increase in similarity of understory community composition of an old-growth ponderosa pine stand that had not been burned since 1923 to that of reference stands (stands with uninterrupted fire regimes, limited grazing, and no logging) due to a low-severity wildfire. They attributed the change to an increase in annual and biennial forbs. In addition, they reported that non-interrupted fire regime sites tend to have greater species richness due to a low ratio of duff to litter. These studies provide insights into short-term changes in understory species, but provide little information regarding long-term changes.

This study was built upon a pre-existing project that was developed in 1972 after a wildfire burned through a ponderosa pine forest in the Coconino National Forest of northern Arizona. The original studies reported the short-term response of understory plant species to fire in terms of composition and production for the years of 1972, 1974, and 1980 (Beaulieu, 1975; Oswald and Covington, 1983, 1984). The objective of this study was to examine changes in species composition and production of understory vegetation since the 1972 Rattle Burn wildfire on the Coconino National Forest near Flagstaff, Arizona. In addition, we attempted to explore how overstory attributes (basal area and canopy cover) contributed to patterns in understory composition and production.

2. Methods

2.1. Study area

The study area was located in the Coconino National Forest 30 km southwest of Flagstaff, Arizona. The elevation ranges from 1900 to 2060 m. Major soils are classified as Alfisols, and include Soldier, McVickers, and Hogg series, which developed from Kaibab limestone and Coconino sandstone parent materials (Oswald and Covington, 1983). The overstory is dominated by ponderosa pine, with a few Gambel oak *(Quercus gambelii* Nutt.), alligator juniper *(Juniperus deppeana* Steud.), white fir (*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Campbell et al., 1977). The climate of the area is characterized by cold winters, mild summers, and moderate humidity (Staudenmaier et al., 2005). Most of the precipitation falls in the form of snow during the winter; the remainder occurs as rain showers mainly in the months of July and August (Campbell et al., 1977). Annual precipitation ranged from 28.5 to 90.4 cm and averaged 56.7 cm during the 33-year period of 1970–2003 (Fig. 1) (Western Regional Climate Center, Desert Research Institute, 2004).

Prior to a logging operation in the spring of 1970, which removed an average of 16 $m^3\ ha^{-1}$ of timber (Beaulieu, 1975), the study site area supported an average of 371 $m^3\ ha^{-1}$ of timber (Campbell et al., 1977). In early May of 1972, the Rattle Burn wildfire burned 286 ha. During the following summer and fall, a post-fire salvage logging operation removed 4366 $m^3\ ha^{-1}$ of timber and the skid trails were seeded with a variety of grasses and forbs (Oswald, 1981). The study area has been grazed by cattle (*Bos taurus* Linnaeus), sheep (*Ovis aries* Linnaeus), mule deer (*Odocoileus hemionus* (Rafinesque)), and elk (*Cervus elaphus* Erxleben) since the 1970s, but no data on grazing intensity are available. Ponderosa pine

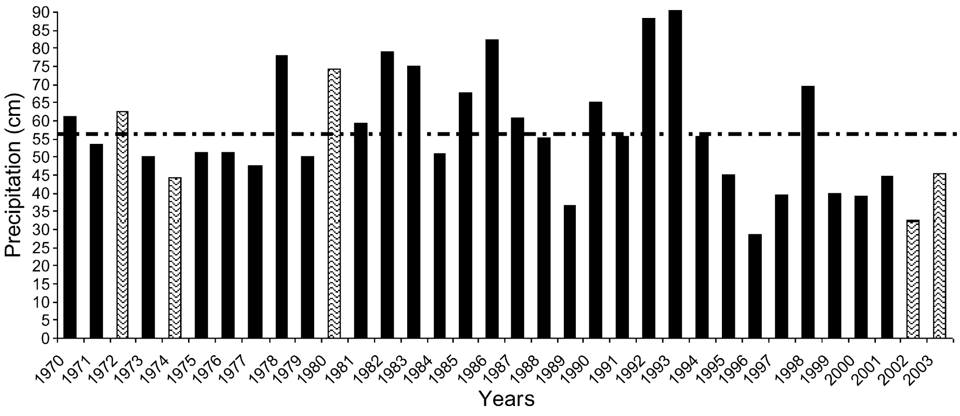

Fig. 1. Total annual (January–December) precipitation at Flagstaff WSO AP, Arizona, from 1970 through 2003 and 33-year average (567 mm; dashed line).

seedlings were planted in some areas of the fire in the spring of 1975 (Campbell et al., 1977), and on severely burned areas (including the plots) in 1983 (James Rolf, USDA Forest Service, Coconino National Forest, personal communication).

2.2. Study establishment

Permanent plots were established with rebar in three watersheds in 1972 after the Rattle Burn wildfire: a high severity burn site (HSWF), a low severity burn site (LSWF), and an unburned site that was later prescribed burned in 1977 (UBPB). According to Beaulieu (1975), in the HSWF site most of the trees were killed by a crown fire and severe surface fire, whereas in the LSWF site, most of the trees survived the surface fire. Campbell et al. (1977) estimated the intensity of the wildfire to be 9000 $kJ^{-1}\ s^{-1}\ m^{-1}$ for the LSWF site and 35,000 $kJ^{-1}\ s^{-1}\ m^{-1}$ for the HSWF site using Byram's formula and measurements from similar stands. In 1974, an additional unburned site (UB) was permanently established with rebar adjacent to the burned area. Within each research site, 30 plots, 404.7 m^2 in area (20.1 m × 20.1 m), were placed along transects, giving a total of 120 plots (4 research sites × 30 plots). The distances between plots along a transect and between transects varied within and among sites. Within each plot, four circular quadrats, 0.89 m^2 in area, were established at 90° angles around each center point at a distance of 7.1 m from the center (Beaulieu, 1975; Oswald, 1981).

2.3. Data collection

Overstory measurements were collected in the summer of 1972 on the three original watershed sites. Diameter at breast height (DBH) was recorded in diameter classes (1.1–3.0, 3.1–5.0, . . ., 33.1–35.0) for all trees within the 90 plots. Tree density and basal area were calculated for each plot. The midpoints of each DBH class were used in determining basal area (Campbell et al., 1977). In July of 2003, DBH of all trees within each of the 90 plots was re-measured. In addition, DBH was measured on the 30 plots of the UB site that was established in 1974. Tree density and basal area (using midpoints of DBH classes) were calculated for each plot. In the center of two randomly selected quadrats in each plot, mean overstory canopy cover was estimated using a spherical densiometer (average of one reading per cardinal direction). Mean canopy cover estimates per plot were used for comparisons.

Following the same measurement protocols used in 1972, 1974, and 1980, we measured two understory response variables: species composition and production. In July and August of 2002 and 2003, understory vegetation within two randomly selected circular quadrats in each plot per site was identified to the species level and clipped. Production was estimated based on oven-dry weight. The samples were dried for 48 h at 69 °C. Dry weights were recorded to the nearest 0.01 g. Species production data were averaged by quadrat ($n = 2$) for analysis. Total production and species composition data were compared with previous data (Beaulieu, 1975; Oswald, 1981) collected from the same plots in July and August of 1972, 1974, and 1980.

2.4. Data analysis

Mean plant production per plot by site for the 5 years studied was analyzed using repeated measures procedure in PROC MIXED (SAS Institute Inc., 1999). The random statement in PROC MIXED was used to examine and model the covariance structure of the general linear model. The model fit criteria, Akaike's Information and Schwarz' Bayesian, were used to select an appropriate covariance structure. The compound symmetric covariance structure was chosen as an appropriate covariance structure (Little et al., 1996). In other words, the underlying assumption of sphericity for repeated measures was satisfied (Zar, 1999). The data were split into two sets due to unequal treatment levels among the 5 years studied. Set one included data from 4 years (1974, 1980, 2002, and 2003) with four levels of treatment (HSWF, LSWF, UBPB, and UB) within each year. Set two included data from 5 years (1972, 1974, 1980, 2002, and 2003) with three levels of treatment (HSWF, LSWF, and UBPB) within each year. When a significant treatment by year interaction was found, we used one-way ANOVA to identify differences among treatments each year. In order to maintain an overall familywise alpha level of 0.05, a Bonferroni adjustment was applied to each one-way ANOVA (Westfall and Young, 1993; Lehman, 1995). Since there were five one-way ANOVA's performed, the familywise alpha was adjusted to 0.01. Tukey's multiple comparison procedure was used to separate treatment means whenever a significant treatment effect was found.

In order to incorporate species composition into the analysis, multi-response permutation procedures (MRPP) was utilized to test the hypothesis of no difference in composition (production by species) between treatments within each year (Zimmerman et al., 1985). A Bonferroni adjustment was applied to each MRPP, in a similar fashion to the one-way ANOVAs, in order to maintain an overall familywise alpha level of 0.05 (Westfall and Young, 1993; Lehman, 1995). Pairwise comparisons were utilized whenever a significant treatment effect was found (McCune and Mefford, 1999). To determine what species are driving the differences among the sites for each specific year, Indicator Species Analysis (Dufrene and Legendre, 1997) was conducted. Significance of indicator values was assessed using a Monte Carlo randomization test based on 10,000 permutations (McCune and Mefford, 1999). Only species that are significant at the 0.05 alpha level and have a INDVAL greater than 25 will be considered as indictor species for a site (Dufrene and Legendre, 1997).

If significant differences were found among the sites in 1972 or 2003 using MRPP, then the Mantel test was used to determine if there was a relationship between the overstory attributes (basal area and canopy cover) and understory attributes (species composition and production) for the year(s) where significant differences occurred. The Mantel test was used to test the hypothesis of no relationship between the overstory matrix and the understory matrix. Significance was assessed at an alpha level of 0.05 using a Monte Carlo randomization test based on 9999 permutations. The standardized Mantel statistic (r), which is the same as the Pearson correlation and also ranges from −1 to 1, was used to measure the strength of the relationship (McCune and Mefford, 1999). When a significant relationship was found, the relationship between each overstory parameter and the understory was examined.

If significant differences were found among the sites in 1972 or 2003 using ANOVA, then simple linear regression was performed for each site to determine if there was a relationship between basal area ($m^2\ ha^{-1}$) or canopy cover (percent) and understory plant production ($kg\ ha^{-1}$) for the year(s) where significant differences occurred. Due to violations of normality and constant variance, transformations were made on the dependent variable (plant production) using the Box-Cox transformations in PROC TRANSREG in SAS (SAS Institute Inc., 1999). The best transformation for the sites of 1972, the HSWF site of 2003, the LSWF and UB sites of 2003, and the UBPB site of 2003 was the $\sqrt[4]{Y}$ 4th root of Y, $1/\sqrt[4]{Y}$, $\sqrt{Y}$, and $\log_e Y$, respectively.

Understory species composition and production data were summarized with detrended correspondence analysis (DCA). Due to the ongoing discussion concerning the use of DCA (Legendre and Legendre, 1998), non-metric multi-dimensional scaling (NMDS) was chosen as a complimentary technique (Økland, 1996; Økland, 1999). The data were arranged as a Q-matrix, in which site-year combinations served as rows and species represented as production ($kg\ ha^{-1}$) served as columns. The species production data were averaged for each site-year combination ($n = 30$). Since DCA was used to describe the data, it was not necessary to account for correlation between the plots for the different years (Legendre and Legendre, 1998). The data were transformed using square-root transformation in order to give equal weight to all species (Romesburg, 1984). The same matrix was used as a secondary matrix in order to produce vectors in a joint plot graph that showed which species were driving the variation of the axes. Only species with a r^2 greater than 0.5 were used. To aid in interpretation of the ordination, Kendall and Pearson correlations with ordination axes were obtained. In order to determine the best solution (dimensionality with lowest final stress) for NMDS, the "slow and thorough" autopilot procedure was utilized. This procedure uses a maximum of 400 iterations, an instability criterion of 0.00001, 6 axes to begin with, 40 real runs, and 50 randomized runs (McCune and Mefford, 1999). Stress is a measure of departure from monotonicity and tends to increase with sample size. Final stress values for ecological data are usually between 10 and 20. In general, values in the lower half of this range are considered reliable solutions (McCune and Grace, 2002). The autopilot mode chose a two-dimensional ordination for the final iterative ordination and used the best ending point in the preliminary analysis as the starting point in the final run. In order to determine the effectiveness of DCA, coefficients of determination (r^2) for each ordination axis (calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix) were obtained. MRPP, ISA, Mantel test, DCA, and NMDS were all performed using PC-ORD (McCune and Mefford, 1999). Sorenson was chosen as the distance measure for MRPP, ISA, Mantel test, and NMDS (Faith et al., 1987; McCune and Mefford, 1999).

3. Results

3.1. Understory plant production

The time by treatment interaction was significant ($P < 0.001$) for the 5 sampling years and the 4 sampling year data sets. In 1972, the first growing season following the wildfire, mean plant production did not differ among treatments ($P = 0.60$; $F = 0.51$; d.f. = 2) (Fig. 2). By 1974, 2 years post-burn, plant production differed among treatments ($P < 0.001$; $F = 13.50$; d.f. = 3) with the LSWF site having significantly higher production than the UB site. In 1980, production on the UB site and the UBPB sites did not differ, but was lower than production on the HSWF site ($P < 0.001$; $F = 6.06$; d.f. = 3). In 2002, even though production levels were low due to regional drought conditions, production on the HSWF site was significantly

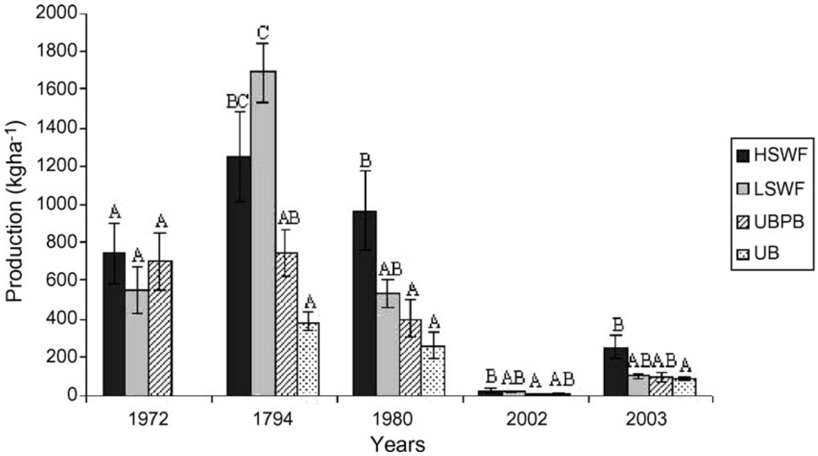

Fig. 2. Mean understory production ($kg\ ha^{-1}$) ($n = 30$) (±S.E.) on high severity wildfire site (HSWF), low severity wildfire site (LSWF), unburned site prescribed burned in 1977 (UBPB), and unburned site (UB). Sites with similar letters did not differ ($P > 0.01$) in total production in that year.

higher than that on the UBPB site ($P = 0.004$; $F = 4.69$; d.f. = 3). In 2003, total understory plant production on the HSWF site was significantly higher than production on the UB site ($P = 0.003$; $F = 4.93$; d.f. = 3).

3.2. Understory plant composition and production

MRPP revealed significant differences among treatments in composition for 1972, 1974, 1980, 2002, and 2003 (alpha = 0.01; $P < 0.001$). In 1972, the HSWF and UBPB sites did not differ significantly from each other but did differ significantly from the LSWF site (Table 1). In 1974, 1980, and 2003, all the sites were significantly different from each other. In 2002, the HSWF and LSWF sites differed significantly from each other and from the UBPB and UB sites, which did not differ significantly from each other.

Indicator Species Analysis revealed that the LSWF and HSWF sites contained most of the species causing differences among the sites within each year (Table 2). In 1972, five species were significantly associated with the LSWF site, whereas only two species were significantly associated with the HSWF/UBPB site-group. There were 10, 3, 3, and 2 species significantly associated with the LSWF, HSWF, UB, and UBPB sites, respectively, in 1974. The LSWF, HSWF, UB, and UBPB sites of 1980 had 4, 2, 1, and 0, respectively, significantly associated species. In 2002, there were 2, 2, and 0 species significantly associated with the HSWF and LSWF sites and the UBPB/UB site-group, respectively. There were 7, 5, 3, and 1 species significantly associated with the HSWF, LSWF, UB, and UBPB sites in 2003, respectively.

The indicator species for the UB site remained relatively constant with Nevada pea (*Lathyrus lanszwertii* var. *leucanthus* Kellogg; (Rydb.) Dorn) as an indicator species in 1974, 1980, and 2003. Bracken fern (*Pteridium aquilinum* (L.) Kuhn) was the only species for the HSWF site that was consistently an indicator species; in 1974, bracken fern was also an indicator species for the UBPB site. The biggest changes in indicator species occurred in the LSWF site. The only consistency for the LSWF site was Cainville thistle (*Cirsium calcareum* (M.E. Jones) Woot. and Standl.) in 1972, 1974, and 1980, squirreltail (*Elymus elymoides* (Raf.) Swezey) in 1972, 1980, and 2003, and Nuttall's linanthus (*Linanthus nuttallii* (Gray) J.M. Porter and L.A. Johnson ssp. *nuttallii*) in all the years studied.

Table 1
P-values for the MRPP pairwise comparisons among the sites for each year, where HSWF = high severity wildfire site, LSWF = low severity wildfire site, UBPB = unburned/prescribed burned site, and UB = unburned site

Site 1	Site 2	1972	1974	1980	2002	2003
HSWF	LSWF	<0.001	<0.001	<0.001	<0.001	<0.001
HSWF	UBPB	0.020	<0.001	0.007	<0.001	<0.001
HSWF	UB	NA	<0.001	<0.001	<0.001	<0.001
LSWF	UBPB	<0.001	<0.001	<0.001	<0.001	<0.001
LSWF	UB	NA	<0.001	<0.001	0.003	<0.001
UBPB	UB	NA	<0.001	<0.001	0.109	<0.001

Table 2
Indicator species for each site-group, determined through MRPP, within each year, where HSWF = high severity wildfire site, LSWF = low severity wildfire site, UBPB = unburned/prescribed burned site, and UB = unburned site

Year	Group	Species	Indicator value	*P*-value
1972	HSWF and UBPB	*Pteridium aquilinum*	53.6	0.0002
	HSWF and UBPB	*Senencio* spp.	31.7	0.0024
	LSWF	*Cirsium calcareum*	25.6	0.0006
	LSWF	*Elymus elymoides*	45.5	0.0011
	LSWF	*Fragaria* spp.	27.4	0.0011
	LSWF	*Linanthus nuttallii*	26.7	0.0004
	LSWF	*Solidago missouriensis*	33.3	0.0001
1974	HSWF	*Amaranthus retroflexus*	39.8	0.0001
	HSWF	*Gayophytum diffusum*	31.3	0.0011
	HSWF	*Senecio actinella*	36.4	0.0001
	LSWF	*Chenopodium album*	30.1	0.0001
	LSWF	*Cirsium calcareum*	29	0.0003
	LSWF	*Linanthus nuttallii*	36.9	0.0001
	LSWF	*Lupinus hilli*	35.9	0.0005
	LSWF	*Packera neomexicana*	35.8	0.0002
	LSWF	*Senecio bigelovii*	50	0.0001
	LSWF	*Solidago missouriensis*	41.7	0.0001
	LSWF	*Taraxacum officinale*	30.1	0.0003
	LSWF	*Verbascum thapsus*	25.2	0.0007
	LSWF	*Vicia americana*	32.3	0.0014
	UBPB	*Muhlenbergia montana*	32.3	0.0001
	UBPB	*Pteridium aquilinum*	33.9	0.0001
	UB	*Carex* spp.	50.7	0.0001
	UB	*Elymus elymoides*	34.7	0.0003
	UB	*Lathyrus lanszwertii*	51.9	0.0001
1980	HSWF	*Epilobium* spp.	41.9	0.0001
	HSWF	*Pteridium aquilinum*	26.4	0.0025
	LSWF	*Cirsium calcareum*	36.4	0.0001
	LSWF	*Elymus elymoides*	32.8	0.0003
	LSWF	*Linanthus nuttallii*	38.6	0.0001
	LSWF	*Solidago velutina*	43.3	0.0001
	UBPB	NONE		
	UB	*Lathyrus lanszwertii*	52	0.0001
2002	HSWF	*Hymenoxys richardsonii*	36.7	0.0001
	HSWF	*Poa pratensis*	55.3	0.0001
	LSWF	*Ceanothus fendleri*	27.3	0.0002
	LSWF	*Linanthus nuttallii*	37.7	0.0001
	UBPB + UB	NONE		
2003	HSWF	*Erigeron divergens*	26.2	0.0048
	HSWF	*Lepidium montanum*	35.5	0.0002
	HSWF	*Plantago patagonica*	40.9	0.0001
	HSWF	*Poa pratensis*	42.4	0.0012
	HSWF	*Pteridium aquilinum*	40.3	0.0001
	HSWF	*Senecio spartioides*	32.9	0.0001
	HSWF	*Thinopyrum intermedium*	59.2	0.0001
	LSWF	*Cirsium wheeleri*	37.3	0.0001
	LSWF	*Elymus elymoides*	31.5	0.0057
	LSWF	*Linanthus nuttallii*	37.8	0.0001
	LSWF	*Packera multilobata*	33.4	0.0023
	LSWF	*Solidago* spp.	33.3	0.0001
	UBPB	*Poa fendleriana*	26	0.0094
	UB	*Carex occidentalis*	40.6	0.003
	UB	*Lathyrus lanszwertii*	67.6	0.0001
	UB	*Lupinus hilli*	52.5	0.0001

3.3. Overstory attributes

Reconstructed pre-fire forest tree density structure of 1972 decreased 86, 99, and 5% from the to the post-logging forest structure of 1972 for the LSWF, HSWF, and UBPB sites, respectively (Table 3). In addition, basal area decreased 55, 94, and 35% for the LSWF, HSWF, and UBPB sites, respectively, for the same time period. Between the post-logged forest structure of 1972 and 2003, tree density for the LSWF and UBPB sites declined 4 and 65%, respectively. In contrast, basal area increased 12 and 5% for the LSWF and UBPB sites, respectively, during this period. For the HSWF site, tree density and basal area increased 3219 and 228%, respectively, for this period. In 2003, the UB site had the most canopy cover and highest quadratic mean diameter; whereas, the HSWF site had the least canopy cover and lowest quadratic mean diameter.

3.4. Overstory–understory relationship

The Mantel test revealed significant relationships between overstory parameters and the understory for 1972 ($P = 0.023$; $r = 0.06$) and 2003 ($P = 0.036$; $r = 0.04$). In 1972, basal area ($P = 0.034$; $r = 0.06$) was significantly correlated with species composition and production; basal area ($P < 0.001$; $r = 0.09$) was also significantly correlated with species composition and production in 2003.

Table 3
Mean overstory attributes ($n = 30$) with 95% confidence limits in parentheses by site and year for the Rattle Burn HSWF = high severity wildfire site, LSWF = low severity wildfire site, UBPB = unburned/prescribed burned site, and UB = unburned site

Site	1972[a]	1972[b]	2003
Tree density (no. ha^{-1})			
LSWF	1836.8 (403.8)	257.8 (73.9)	248.7 (55.1)
HSWF	1575.7 (377.7)	16.5 (14.0)	547.7 (121.0)
UBPB	1592.1 (338.1)	1519.7 (339.3)	524.7 (123.3)
UB[c]	NA	NA	401.1 (62.7)
Basal area (m^2 ha^{-1})			
LSWF	52.5 (6.9)	23.5 (5.3)	20.7 (2.9)
HSWF	46.4 (5.9)	2.9 (2.8)	9.5 (1.5)
UBPB	55.9 (6.1)	36.5 (5.3)	34.6 (2.2)
UB[c]	NA	NA	37.1 (2.5)
Quadratic mean diameter (QMD) (m^2)			
LSWF	19.1	34.1	32.6
HSWF	19.4	47.3	14.9
UBPB	21.1	17.5	29.0
UB[c]	NA	NA	34.3
Canopy cover[d] (%)			
LSWF	NA	NA	55.3 (4.4)
HSWF	NA	NA	23.8 (6.8)
UBPB	NA	NA	47.4 (3.8)
UB	NA	NA	64.1 (3.5)

[a] Pre-logging determined from stumps, burned trees (for LSWF and HSWF), and live trees.

[b] Post-logging for UBPB and post-salvage for LSWF and HSWF determined from live trees.

[c] Overstory data were not collected for 1974 UB site in 1972.

[d] Canopy cover data not available for 1972.

Simple linear regression with a square root transformation on understory production showed significantly negative relationships between understory production and basal area (liberal $P \geq 0.001$; $r^2 = 0.31$) and canopy cover (liberal $P \geq 0.022$; $r^2 = 0.17$) for the LSWF site in 2003. There was not a significant relationship between understory production and basal area in 1972.

3.5. Summarization of species composition and production

Since the 1972 wildfire, 112 species have been identified on the sites. There were 27 species that were newly identified in 2002 and/or 2003 that were not previously documented. Conversely, 27 species reported in 1972, 1974, and/or 1980 were not found in 2002 or 2003. In general, total understory production has decreased over time, with peak production occurring in 1974 and lowest production occurring in 2002. Dominant species patterns have also changed on the sites through time (Table 2 and Appendix A). For instance, there were 16 species not observed in 2002 and 13 species not observed in 2003 that were dominant in 1972, 1974, and/or 1980 (Appendix A). A majority of the dominant species, 41%, were from the Asteraceae family. Nine of the dominant species in 1980 and/or 2003 were exotics, including cheatgrass (*Bromus tectorum* L.), squirreltail, spreading groundsmoke (*Gayophytum diffusum* Torr. and Gray), yellow hawkweed (*Hieracium fendleri* Schultz-Bip.), prairie junegrass (*Koeleria macrantha* (Jedeb.) J.A. Schultes), lobeleaf groundsel (*Packera multilobata* (Torr. and Gray ex Gray) W.A. Weber and A. Löve), common sheep sorrel (*Rumex acetosella* L.), wooton's ragwort (*Senecio wootonii* Greene), and Missouri goldenrod (*Solidago missouriensis* Nutt.).

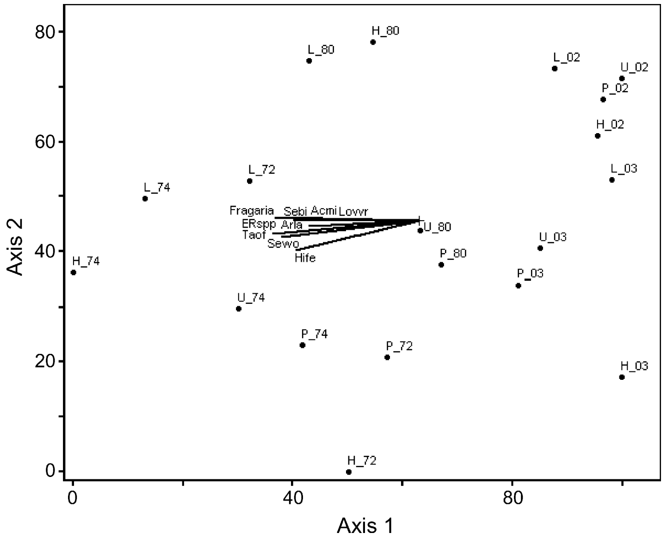

Fig. 3. DCA joint plot graph based on understory species composition and production for various site-year combinations (H = high severity wildfire site, L = low severity wildfire site, P = unburned turned into a prescribed burn site, and U = unburned site; 72 = 1972, 74 = 1974, 80 = 1980, 02 = 2002, and 03 = 2003) with the highly correlated species shown as vectors in relation to Axis 1 (Hife = *Hieracium fendleri*, Sewo = *Senecio wootonii*, Taof = *Taraxacum officinale*, Fr = *Fragaria* spp., Er = *Erigeron* spp., Arla = *Arenaria lanuginosa*, Sebi = *Senecio bigelovii*, Lowr = *Lotus wrightii*, and Acmi = *Achillea millefolium* var. *occidentalis*).

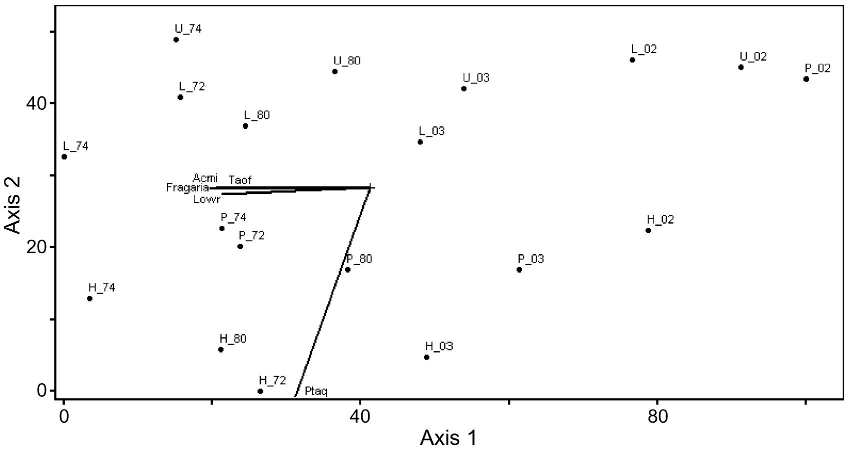

Fig. 4. NMDS joint plot graph based on understory species composition and production for various site-year combinations (H = high severity wildfire site, L = low severity wildfire site, P = unburned turned into a prescribed burn site, and U = unburned site; 72 = 1972, 74 = 1974, 80 = 1980, 02 = 2002, and 03 = 2003) with the highly correlated species shown as vectors in relation to Axis 1 (Fragaria = *Fragaria* spp., Acmi = *Achillea millefolium* var. *occidentalis*, Lowr = *Lotus wrightii*, Taof = *Taraxacum officinale*) and to Axis 2 (Ptaq = *Pteridium aquilinum*).

Axis 1 of the DCA graph accounted for 34% of the variation among the site-year combinations (Fig. 3). Common dandelion (*Taraxacum officinale* G.H. Weber ex Wiggins) ($r^2 = 0.71$), strawberry (*Fragaria* spp. L.) ($r^2 = 0.7$), Wooton's ragwort ($r^2 = 0.67$), fleabane (*Erigeron* spp. L.) ($r^2 = 0.61$), yellow hawkweed ($r^2 = 0.59$), spreading sandwort (*Arenaria lanuginosa* (Michx.) Rohrb.) ($r^2 = 0.53$), nodding ragwort (*Senecio bigelovii* Gray) ($r^2 = 0.51$), Wright's deervetch (*Lotus wrightii* (Gray) Greene) ($r^2 = 0.51$), and western yarrow (*Achillea millefolium* var. *occidentalis* L.; D.C.) ($r^2 = 0.5$) were negatively correlated with Axis 1.

The final stress for the two-dimensional NMDS ordination was 8.87. The proportion of variance explained for each ordination axis was 76.3% for Axis 1 and 11.8% for Axis 2, thus explaining 88.1% of total variation. Axis 1 of NMDS was very similar to that of DCA, and therefore was interpreted the same way (Fig. 4). Axis 2 of NMDS was negatively correlated with bracken fern ($r^2 = 0.76$).

4. Discussion

Data collected 30 years after the Rattle Burn, a May wildfire in northern Arizona, document a decline in understory production compared to the first few years post-burn (Campbell et al., 1977; Oswald, 1981; Oswald and Covington, 1983, 1984). However, this could be mainly attributed to the drought that started in 1999 and persisted through the years studied. In general, greater production occurred in 2003 than in 2002, but this may be due to a greater amount of precipitation in 2003. In fact, 2002 had the 2nd lowest precipitation on record for the 34-year precipitation record (Fig. 1). The drought also affected the species composition in 2002. Most of the dominant species within the other years were not observed in 2002 or 2003 (Appendix A). For instance, redroot amaranth (*Amaranthus retroflexus* L.), Missouri goldenrod and Canadian horseweed (*Conyza canadensis* (L.) Cronq.), which were dominant in the HSWF, LSWF, and both the HSWF and LSWF sites, respectively, of 1974, were not captured in 2002 or 2003. In 1980, broom snakeweed (*Gutierrezia sarothra* (Pursh) Britt. and Rusby), western wheatgrass (*Pascopyrum smithii* (Rybd.) A. Löve), Flagstaff ragwort (*Senecio actinella* Greene), and threenerve goldenrod (*Solidago velutina* D.C.) were dominant in the HSWF, LSWF, UBPB, and LSWF sites, respectively, but were not captured in 2002 or 2003. Lambsquarters (*Chenopodium album* L.) was dominant in the LSWF and UBPB sites of 1974 and not captured in 2002 or 2003.

Understory production was not significantly different between the unburned site and the burned sites the first growing season (2 months) after the fire. This is in agreement with Zimmerman et al. (1985), Andariese and Covington (1986), and Wienk et al. (2004). Wienk et al. (2004) attributed non-significant difference in production to the time required for colonization by pioneer species, since the species that responded the second growing season were not found in the seed bank. This rationale may also explain the non-significant difference encountered in this study. Assuming the unburned site should have greater production than the burned sites, the non-significant difference may also be partially explained by bracken fern's ability to replace fronds lost to fire, or other agents, with its reservoir of dormant buds. Production of bracken fern would have contributed greatly to the overall production of the burned sites, thus reducing the differences in production of the sites (Ferguson and Boyd, 1988).

Although none of the sites were significantly different in terms of production in 1972, the HSWF and UBPB sites were significantly different from the LSWF site in terms of composition. The HSWF and UBPB sites were dominated by bracken fern and ragworts (*Senecio* spp. L.), whereas the LSWF site was dominated by squirreltail, Missouri goldenrod, strawberry, Nuttall's linanthus, and Cainville thistle. Bracken fern initially invades a disturbed (burned, grazed, or logged) site by windblown spores (Ferguson and Boyd, 1988) and, once established, sprouts prolifically from deeply buried rhizhomes (Skutch, 1929; Ferguson and Boyd, 1988). Since bracken fern is known to occur on burned and logged forests in this region (Parker, 1972), it is possible that bracken fern became established in the sites due to the logging that occurred 2 years before the wildfire. The existence of bracken fern within these sites cannot be attributed to the 1972 wildfire or the 1977 prescribed burn, but it is possible that fire may have aided in bracken fern's dominance in the UBPB and HSWF sites.

In addition to western bracken fern, which is known to occur in disturbed forests in this region (Parker, 1972) and sprouts prolifically from deeply buried rhizhomes (Skutch, 1929), a number of other pioneering plants made up the majority of the 1974 plant production on severely burned areas of the Rattle Burn. This list included exotic species such as redroot amaranth and lambsquarters as well as native species such as Wooton's ragwort and spreading groundsmoke. Lambsquarters and spreading groundsmoke are often reported as occurring on burned sites in the region (e.g., Crawford et al., 2001; Laughlin et al., 2004). On low severity burned areas, the second year plant community included a number of native and exotic plants that commonly occur in burned areas. The exotic invasive, common mullein (*Verbascum thapsus* L.), as well as the native ruderal, Canadian horseweed, are frequently observed on burned areas in the southwest (Crawford et al., 2001; Sieg et al., 2003), and are especially common in seedbanks of forests with a long history of disturbance (Korb et al., 2005). The increases in production reported for the same sites in earlier studies (Oswald and Covington, 1983, 1984) follow other results (Ffolliott and Clary, 1974; Pearson et al., 1972).

The plant production of the LSWF site of 1974 and the HSWF site of 1980 and 2003 was significantly greater than the unburned sites of the corresponding years. There appears to be a lingering effect of fire upon the understory production 30 years after the Rattle Burn wildfire, similar to that documented in the southwest (Ffolliott et al., 1977; Lowe et al., 1978). Ffolliott et al. (1977) reported that increases from 3.4 kg ha^{-1} before prescribed burning to 45.4 kg ha^{-1} one year post-burn were sustained in the 11th post-fire year in a relatively dense forest. Lowe et al. (1978) reported that basal cover of grasses remained two to three times greater for up to 20 years on areas burned by wildfires compared to an unburned area.

All the sites differed from each other in species composition in 1974, 1980, and 2003. For instance, the only similarity in the five most dominant species among sites in 1974 were: western yarrow for the UBPB and UB sites, lambsquarters for the LSWF and UBPB sites, Canadian horseweed for the HSWF and LSWF sites, and bracken fern for the HSWF and UBPB sites. In 1980, the only similarity in the five most dominant species among sites were: western yarrow for the HSWF and UB sites, small-leaf pussytoes (*Antennaria parvifolia* Nutt.) for the LSWF and UBPB sites, Nevada pea for the UBPB and UB sites, Hill's lupine (*Lupinus hilli* Greene) for the LSWF and UB sites, bracken fern for the HSWF and UBPB sites, and muttongrass (*Poa fendleriana* (Steud.) Vasey) for all the sites. In 2003, the similarity in the five most dominant species among sites consisted of small-leaf pussytoes for the LSWF, UBPB, and UB sites, bracken fern for the HSWF, LSWF, and UBPB sites, muttongrass for the UBPB and UB sites, and Kentucky bluegrass (*Poa pratensis* L.) for the HSWF, LSWF, and UBPB sites. This implies that fire has altered the dominance pattern of the understory species of these sites. However, since this study was impacted by drought in 2002 and 2003, it is difficult to determine if fire has in fact changed the understory species dominance patterns of these sites.

The Mantel test revealed a significant, but weak relationship between basal area and species composition and production for 1972 and 2003. Regression also showed a significant relationship between basal area and species production in 1972 and 2003, as well as between canopy cover and species production in 2003. Similar overstory–understory vegetation relationships have been reported by Clary and Ffolliott (1966), Moore and Deiter (1992), Naumberg et al. (2001), and Wienk et al. (2004).

As reflected by characteristics of the species, the negative correlation between common dandelion and western yarrow with Axis 1 of DCA and NMDS may be interpreted as a lack of disturbance, in the form of fire and thinning, since the 1972 wildfire and the 1977 prescribed burn. Common dandelion, the second most negatively correlated species to Axis 1, was considered an indicator of burned areas in Grand Canyon National Park (Huisinga et al., 2005), but may peak in production the first year or two following prescribed fires in Douglas-fir (*P. menziesii* (Mirbel) forests in south-central Idaho (Lyon, 1966). The decline of common dandelion in the sites of 2002 and 2003 reflects a time lag response since the 1972 wildfire, as well as the droughty conditions. Other negatively correlated species, such as western yarrow also increase with fire and then decrease with time since the fire (Parker, 1972, Humphrey, 1984) and Wright's deervetch increased in abundance after overstory removal in piñon-juniper woodlands in New Mexico (Kleintjes et al., 2004).

5. Conclusions

None of the sites used in this study represent the historic fire return intervals associated with ponderosa pine forests of the southwestern United States, but instead represent conditions where the historic disturbance vector (fire) has been reduced for over a century. In severely burned areas of the 1972 Rattle Burn, nearly complete elimination of the forest canopy stimulated understory production levels to exceed that found on unburned areas by two-fold during the third growing season, four-folds during the ninth growing season, and two-folds during the 32nd growing season. Even in lightly burned areas, removal of litter cover stimulated understory production levels to exceed that found on unburned areas by two-fold during the third growing season. Thirty years after the wildfire, total plant production has declined dramatically on both burned and unburned areas and the dominant species patterns have been altered on all the sites. However, long-term drought conditions may have played a major role in shaping these outcomes. Due to the effect drought may have played in shaping understory species dominance, it would be good to continue to monitor the sites to determine the differences are actually due to the fire. In addition, the role of grazing cannot be underestimated. No evaluation of grazing pressure has been conducted on these sites and thus the effects of grazing in shaping the outcome on these sites are unknown. Even though extrapolation of these results to other areas should be made cautiously and long-term studies like these are important, more long-term studies need to be conducted that take into consideration climate change and grazing patterns.

From the results of this study, land managers in similar ecosystems could anticipate an effect of fire even 30 years after the event. Depending upon management objectives, these lingering effects may prove beneficial. Since domestic grazing is common in such ecosystems, a fire-grazing interaction may be expected and could produce similar to results of this study. The potential impact of climate change may be observed in the variation in production and composition reported here, even though these results do not necessarily reflect long-term change in climate conditions.

Acknowledgements

This project was a cooperative agreement between US Forest Service Rocky Mountain Research Station and Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University. We sincerely thank Dr. Jim Fowler for help in identification of plants. We also thank Kim Massey and April Thomas for their assistance in the field. We are grateful to Noah Barstatis, Rudy King, and Dr. Greg Miller for their valuable comments on earlier versions of the manuscript. We are especially grateful to Dr. Carolyn Sieg for her invaluable contributions throughout the project. In addition, we are indebted to Peter Fulé and the anonymous reviewers for their invaluable contribution to the manuscript.

Appendix A

Mean plant production (kg ha^{-1}) with S.E. in parentheses ($n = 30$) of major plant species in 1972, 1974, 1980, 2002, and 2003, on high severity wildfire (HSWF), low severity wildfire (LSWF), unburned/prescribed burned in 1977 (UBPB), and an unburned site (UB)[a]. The five most dominant for each site-year combination is in bold. Species with a trace amount for that site-year combination are represented by a T. Species not captured during data collection for that site-year combination are represented by a dash.

Species	1972				1974			
	HSWF	LSWF	UBPB	UB[a]	HSWF	LSWF	UBPB	UB
Forbs								
Achillea millefolium	0.5(0.4)	24.7(13.4)	11.2(7.7)		9.0(5.5)	69.7(29.0)	**44.0(22.0)**	**24.6(7.2)**
Amaranthus retroflexus	0.1(0.1)	–	1.3(1.3)		**150.7(46.7)**	0.8(0.6)	–	–
Antennaria parvifolia	0.2(0.2)	**29.1(10.4)**	21.8(9.2)		3.8(2.5)	35.0(18.7)	**52.3(19.7)**	24.2(10.9)
Chenopodium album	0.1(0.1)	0.9(0.8)	2.2(2.2)		11.3(7.1)	**94.39(29.7)**	**16.8(16.8)**	3.1(3.0)
Conyza canadensis	–	–	0.6(0.4)		**194.8(48.5)**	**164.5(88.6)**	–	–
Draba asprella	0.5(0.5)	1.4(0.7)	0.4(0.4)		–	4.1(2.2)	1.4(1.4)	1.3(0.7)
Erigeron divergens	–	–	–		–	–	–	–
Erigeron formosissimus	–	–	–		–	–	–	–
Erigeron spp.	0.5(0.5)	**72.6(48.0)**	1.4(1.0)		9.1(4.3)	49.0(17.6)	4.1(2.9)	**25.5(5.9)**
Gayophytum diffusum	–	–	1.2(0.7)		**82.4(26.1)**	48.6(14.8)	0.5(0.2)	–
Hymenoxys richardsonii	–	–	–		–	–	–	–
Lathyrus lanszwertii	7.3(1.9)	14.5(3.8)	18.6(4.2)		2.6(1.0)	13.5(3.2)	7.8(1.5)	**29.9(4.4)**
Linanthus nuttallii	–	10.6(4.2)	–		–	31.0(9.2)	0.3(0.3)	2.2(1.2)
Lupinus hilli	1.7(1.2)	9.2(3.7)	3.8(1.9)		0.3(0.3)	52.8(15.8)	1.4(0.5)	9.4(2.6)
Plantago patagonica	–	–	–		–	–	–	–
Plantago spp.	–	0.3(0.2)	**39.3(39.3)**		–	–	–	–
Pteridium aquilinum	**477.5(133.3)**	11.5(8.7)	**401.8(103.3)**		**394.6(169.4)**	66.7(46.3)	**477.4(112.3)**	–
Rumex acetosella	**24.3(24.3)**	–	T		0.1(0.1)	–	–	–
Senecio actinella	–	–	16.3(14.7)		54.2(16.5)	–	0.5(0.5)	–
Senecio bigelovii	**64.0(37.3)**	**37.2(24.7)**	–		–	**179.1(50.0)**	–	–
Senecio spartioides	**24.5(24.5)**	–	0.2(0.2)		–	–	0.5(0.5)	–
Senecio spp.	1.1(0.5)	–	14.3(4.7)		5.1(3.7)	22.2(8.2)	**37.8(12.9)**	9.7(4.5)
Senecio wootonii	14.1(13.4)	15.6(5.9)	5.4(3.3)		**145.1(112.2)**	52.7(29.8)	16.2(6.6)	0.4(0.3)
Solidago missouriensis	–	7.7(3.1)	–		–	**141.6(42.9)**	0.9(0.6)	4.6(2.4)
Solidago spp.	–	0.9(0.4)	–		T	–	–	–
Solidago velutina	–	0.6(0.6)	0.1(0.1)		–	–	–	–
Verbascum thapsus	–	**33.7(33.7)**	**37.2(25.8)**		26.5(14.1)	**174.4(79.4)**	–	6.7(5.3)
Vicia americana	2.54(1.8)	7.9(1.9)	7.8(2.2)		2.3(1.2)	25.7(7.2)	7.2(2.1)	10.0(2.9)
Graminoids								
Carex occidentalis	–	–	–		–	–	–	–
Carex spp.	1.7(0.8)	7.9(4.9)	**31.4(13.6)**		11.4(4.9)	14.8(5.1)	10.9(5.7)	**47.8(9.6)**
Elymus elymoides	2.9(2.0)	**94.9(30.0)**	1.9(0.7)		12.9(5.1)	38.1(13.7)	5.6(2.2)	**105.5(25.4)**
Muhlenbergia montana	–	7.5(6.8)	6.9(3.5)		–	T	4.5(1.7)	0.2(.02)
Muhlenbergia spp.	**81.0(53.5)**	–	1.0(1.0)		–	–	–	–
Pascopyrum smithii	–	–	–		–	–	–	–

Appendix A (*Continued*)

Species	1972				1974			
	HSWF	LSWF	UBPB	UB[a]	HSWF	LSWF	UBPB	UB
Poa fendleriana	–	–	–		–	–	–	–
Poa pratensis	3.0(1.5)	19.9(13.2)	**30.9(12.3)**		–	3.4(1.7)	5.9(4.3)	1.4(1.4)
Thinopyrum intermedium	–	–	–		–	–	–	–
Shrubs								
Ceanothus fendleri	10.0(5.6)	0.4(0.2)	–		28.7(11.0)	27.4(10.0)	5.3(3.9)	–
Gutierrezia sarothrae	–	–	–		–	–	–	–

Species	1980				2002			
	HSWF	LSWF	UBPB	UB	HSWF	LSWF	UBPB	UB
Forbs								
Achillea millefolium	**58.0(35.1)**	8.8(5.6)	2.2(2.2)	**14.4(5.7)**	0.4(0.3)	0.4(0.2)	**0.1(0.1)**	0.2(0.1)
Amaranthus retroflexus	0.3(0.3)	–	–	–	–	–	–	–
Antennaria parvifolia	0.2(0.2)	**37.2(20.0)**	**10.8(5.6)**	4.9(2.1)	–	0.6(0.3)	**0.5(0.2)**	**0.4(0.4)**
Chenopodium album	–	–	–	–	–	–	–	–
Conyza canadensis	0.4(0.3)	–	–	–	–	–	–	–
Draba asprella	0.6(0.6)	2.9(1.8)	0.1(0.1)	0.2(0.1)	0.5(0.3)	0.9(0.5)	–	**0.4(0.2)**
Erigeron divergens	–	–	–	–	–	–	–	–
Erigeron formosissimus	–	–	–	–	0.2(0.1)	–	–	–
Erigeron spp.	11.8(8.2)	10.0(5.5)	–	2.6(1.2)	–	–	–	–
Gayophytum diffusum	13.6(6.4)	2.5(1.3)	2.0(0.9)	–	–	–	–	T
Hymenoxys richardsonii	–	0.3(0.2)	–	–	**3.4(1.3)**	–	–	–
Lathyrus lanszwertii	0.1(0.1)	6.4(1.8)	**10.6(3.5)**	**60.6(13.8)**	0.1(0.1)	T	T	0.1(0.0)
Linanthus nuttallii	–	36.4(14.8)	–	1.3(0.9)	0.2(0.2)	**1.4(0.5)**	–	0.1(0.1)
Lupinus hilli	0.4(0.3)	**44.5(18.4)**	3.8(1.9)	**69.2(37.1)**	T	T	–	0.1(0.1)
Plantago patagonica	–	–	–	–	–	–	–	–
Plantago spp.	0.5(0.5)	–	–	–	–	–	–	–
Pteridium aquilinum	**649.9(208.0)**	24.6(20.1)	**305.7(100.5)**	4.4(4.4)	**9.5(8.5)**	–	**0.1(0.1)**	–
Rumex acetosella	–	2.5(2.5)	T	2.3(2.3)	–	–	–	–
Senecio actinella	2.8(1.6)	2.1(2.1)	**11.4(6.8)**	0.4(0.3)	–	–	–	–
Senecio bigelovii	8.0(4.4)	32.6(20.1)	–	–	–	–	–	–
Senecio spartioides	–	–	–	–	–	–	–	–
Senecio spp.	–	–	–	–	0.1(0.1)	.01(0.1)	–	–
Senecio wootonii	1.1(1.0)	1.4(1.0)	6.2(2.2)	5.5(3.3)	–	–	–	–
Solidago missouriensis	3.4(2.9)	14.3(10.7)	0.4(0.3)	1.4(1.1)	–	–	–	–
Solidago spp.	–	–	–	–	–	–	–	–
Solidago velutina	–	**37.5(11.3)**	–	–	–	–	–	–
Verbascum thapsus	–	10.9(6.5)	–	–	0.2(0.2)	–	–	–
Vicia americana	1.4(0.7)	3.7(1.4)	4.6(1.6)	**33.4(25.9)**	0.1(0.1)	0.4(0.4)	T	T
Graminoids								
Carex occidentalis	–	–	–	–	–	–	–	–
Carex spp.	–	–	–	–	–	–	–	–
Elymus elymoides	3.2(2.0)	18.8(5.0)	0.4(0.2)	4.3(1.5)	–	–	–	–
Muhlenbergia montana	–	1.9(1.4)	–	–	–	**4.7(3.7)**	–	**3.3(1.7)**
Muhlenbergia spp.	–	–	–	–	–	–	–	–
Pascopyrum smithii	26.1(11.7)	**43.5(25.2)**	–	–	–	–	–	–
Poa fendleriana	**28.0(8.6)**	**42.8(9.3)**	**29.5(6.4)**	**28.5(6.9)**	**3.0(0.8)**	**6.9(1.6)**	**3.9(0.9)**	**5.4(1.7)**
Poa pratensis	3.4(1.9)	3.9(2.6)	–	6.8(4.5)	**10.3(2.4)**	**4.3(2.3)**	**0.2(0.1)**	**0.3(0.2)**
Thinopyrum intermedium	–	–	–	–	–	–	–	–
Shrubs								
Ceanothus fendleri	**31.2(11.9)**	18.4(6.7)	–	–	**0.6(0.4)**	**1.7(0.6)**	–	–
Gutierrezia sarothrae	**52.4(25.4)**	–	–	–	–	–	–	–

Species	2003			
	HSWF	LSWF	UBPB	UB
Forbs				
Achillea millefolium	1.3(0.8)	1.5(0.6)	0.1(0.1)	1.0(0.4)
Amaranthus retroflexus	–	–	–	–
Antennaria parvifolia	–	**15.6(7.3)**	**3.9(1.5)**	**4.0(3.0)**
Chenopodium album	–	–	–	–
Conyza canadensis	–	–	–	–

Appendix A (*Continued*)

Species	2003			
	HSWF	LSWF	UBPB	UB
Draba asprella	0.3(0.3)	1.7(1.4)	–	0.2(0.1)
Erigeron divergens	**4.4(2.5)**	1.7(1.2)	–	1.2(1.2)
Erigeron formosissimus	0.5(0.3)	**4.3(2.2)**	–	0.9(0.5)
Erigeron spp.	–	–	T	–
Gayophytum diffusum	0.1(0.1)	0.5(0.4)	0.1(0.1)	–
Hymenoxys richardsonii	–	–	–	–
Lathyrus lanszwertii	0.3(0.1)	2.6(0.7)	0.6(0.3)	**25.6(5.7)**
Linanthus nuttallii	0.4(0.4)	4.1(1.2)	–	0.3(0.1)
Lupinus hilli	0.1(0.1)	2.0(0.7)	**1.8(1.5)**	**27.1(8.3)**
Plantago patagonica	**5.1(1.9)**	0.3(0.2)	–	–
Plantago spp.	–	–	–	–
Pteridium aquilinum	**175.3(60.5)**	**5.4(3.1)**	**79.3(24.6)**	1.1(1.1)
Rumex acetosella	1.4(0.8)	T	–	–
Senecio actinella	–	–	–	–
Senecio bigelovii	–	–	–	–
Senecio spartioides	3.5(2.5)	0.1(0.1)	–	–
Senecio spp.	–	–	–	–
Senecio wootonii	0.1(0.1)	0.1(0.1)	0.3(0.2)	T
Solidago missouriensis	–	–	–	–
Solidago spp.	T	**5.8(2.5)**	0.2(0.1)	0.4(0.2)
Solidago velutina	–	–	–	–
Verbascum thapsus	0.3(0.2)	–	–	–
Vicia americana	0.9(0.3)	2.7(0.7)	0.2(0.1)	2.9(1.2)
Graminoids				
Carex occidentalis	3.0(1.0)	1.9(0.7)	–	8.6(4.4)
Carex spp.	–	–	–	–
Elymus elymoides	1.4(0.7)	3.9(1.1)	0.3(0.3)	1.8(0.5)
Muhlenbergia montana	–	4.1(3.1)	–	1.6(0.9)
Muhlenbergia spp.	–	–	–	–
Pascopyrum smithii	–	–	–	–
Poa fendleriana	1.4(0.7)	3.9(1.5)	**5.5(1.4)**	**3.3(1.2)**
Poa pratensis	**27.0(9.2)**	**15.1(4.8)**	**1.6(0.8)**	3.0(1.1)
Thinopyrum intermedium	**13.2(2.8)**	2.4(1.5)	–	–
Shrubs				
Ceanothus fendleri	0.9(0.6)	2.2(1.0)	–	–
Gutierrezia sarothrae	–	–	–	–

[a] Data are not available for the unburned site in 1972.

References

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, R.C., Loucks, O.L., Swain, A.M., 1968. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. Ecology 50, 255–263.

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

Campbell, R.E., Baker, Jr., M.B., Ffolliott, P.F., Larson, F.R., Avery, C.C., 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-191.

Clary, W.P., Ffolliott, P.F., 1966. Differences in herbage–timber relationships between thinned and unthinned ponderosa pine stands. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Note RM-74.

Clary, W.P., Ffolliott, P.F., Jameson, D.A., 1968. Relationship of different forest floor layers to herbage production. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-123.

Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monogr. 30, 129–164.

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. Vegetation Sci. 12, 261–268.

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

Dieterich, J.H., 1980. Chimney Spring forest fire history. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-220.

Dufrene, 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., Belbi, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Ferguson, D.E., Boyd, R.J., 1988. Bracken fern inhibition of conifer regeneration in northern Idaho. USDA Forest Service, Intermountain Research Station, Research Paper INT-388.

Ffolliott, P.F., Clary, W.P., 1974. Predicting herbage production from forest growth in Arizona ponderosa pine. Proc. Agric. Ariz. 26 (3), 3–5.

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

Foxx, T.S., 1994. Vegetation succession after the La Mesa fire at Bandelier National Monument. In: Allen, C.D., (tech., ed.,), Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium. USDA Forest Service, Rocky Mountain Forest, Range Experiment Station, General Technical Report, RM-GTR-286, pp. 47–69.

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

Goodwin, K.M., Sheley, R.L., 2001. What to do when fires fuel weeds. Rangelands 23, 15–21.

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

Humphrey, L.D., 1984. Patterns and mechanisms of plant succession after fire on Artemisia-grass sites in southeastern Idaho. Vegetatio 57, 91–101.

Huisinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on ground-flora in a mixed conifer forest. J. Torrey Bot. Soc. 132, 590–601.

Kleintjes, P.K., Jacobs, B.F., Fettig, S.M., 2004. Initial response of butterflies to an overstory reduction and slash mulching treatment of a degraded piñon-juniper woodland. Restor. Ecol. 12, 231–238.

Krueger, W.C., Winward, A.H., 1974. Influence of cattle and big game grazing on understory structure of a douglas fir-ponderosa pine-kentucky bluegrass community. J. Range Manage. 27, 450–453.

Korb, J.E., Springer, J.D., Powers, S.R., Moore, M.M., 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: clues to site history and restoration potential. Appl. Veg. Sci. 8, 103–112.

Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Springer, J.D., Gildar, C.N., Green, A.M., Covington, W.W., 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. For. Ecol. Manage. 199, 137–152.

Lehman, R.S., 1995. Statistics in the Behavioral Sciences: A Conceptual Introduction. Brooks/Cole Publishing Company, Pacific Grove, CA.

Legendre, P., Legendre, L., 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Little, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute Inc., Clary, NC.

Lowe, P.O., Ffolliott, P.F., Dieterich, J.H., Patton, D.R., 1978. Determining potential wildlife benefits from wildfire in Arizona ponderosa pine forests. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-52.

Lyon, L.J., 1966. Initial vegetal development following prescribed burning of Douglas-fir in south-central Idaho. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-29.

Madany, M.H., West, N.E., 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park. Utah. Ecol. 64, 661–667.

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.

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

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

Moore, M.M., Deiter, D.A., 1992. Stand density index as a predictor of forage production in northern Arizona pine forest. J. Range Manage. 45, 267–271.

Moore, M.M., Huffman, D., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. For. Sci. 50, 162–176.

Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. Rangeland Ecol. Manage. 59, 135–144.

Naumberg, E., DeWald, L.E., Kolb, T.E., 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forest. Can. J. Bot. 79, 1001–1009.

Økland, R.H., 1996. Are ordination and constrained ordination alternative or complimentary strategies in general ecological studies? J. Vegetation Sci. 7, 289–292.

Økland, R.H., 1999. On the variation explained by ordination and constrained ordination axes. J. Vegetation Sci. 10, 131–136.

Oswald, B.P., 1981. Understory succession following a wildfire in southwestern ponderosa pine. Thesis, Northern Arizona University, Flagstaff, AZ.

Oswald, B.P., Covington, W.W., 1983. Changes in understory production following a wildfire in southwestern ponderosa pine. J. Range Manage. 36, 507–509.

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

Parker, K.F., 1972. An Illustrated Guide to Arizona Weeds. The University of Arizona Press, Tucson, AZ.

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

Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. Introduction to Wildland Fire, Second ed. John Wiley and Sons, New York, NY.

Romesburg, H.C., 1984. Cluster Analysis for Researchers. Lifetime Learning Publications, Belmont, CA.

SAS Institute, 1999. The SAS System, Version 8.02. SAS Institute, Inc., Cary, NC.

Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic invasive plants. In: Friederici, P. (Ed.), Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, DC, pp. 251–268.

Skutch, A.F., 1929. Early stages of plant succession following forest fires. Ecology 10, 177–190.

Staudenmaier, Jr., M., Preston, R., Sorenson, P., 2005. Climate of Flagstaff, Arizona. U.S. Department of Commerce, National Oceanic and Atmospheric Association, Technical Memorandum NWS WR-273.

Wienk, C.L., Sieg, C.H., McPherson, G.R., 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. For. Ecol. Manage. 192, 375–393.

Western Regional Climate Center, Desert Research Institute, 2004. Monthly precipitation, Flagstaff WSO AP, Arizona (http://www.dri.edu/cgi-bin/cliMONtpre.pl?azflag). Desert Research Institute, Reno, NV.

Westfall, P.H., Young, S.S., 1993. Resampling-Based Multiple Testing: Examples and Methods for *p*-Value Adjustment. John Wiley and Sons, New York, NY.

Wright, H.A., Bailey, A.W., 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, New York, NY.

Zar, J.H., 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, NJ.

Zimmerman, G.M., Goetz, H., Mielke Jr., P.W., 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66, 606–611.

Zimmerman, G.T., Neuenschwander, L.F., 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/ninebark habitat type. J. Range Manage. 37, 104–110.