

MULTIPLE PATHWAYS OF POST-FIRE SUCCESSION IN MESA VERDE NATIONAL PARK, SOUTHWESTERN COLORADO

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Resource Management

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Abstract. Multiple pathways of succession were evident eight years following a severe 1200-ha fire in Mesa Verde National Park (MVNP). The 1989 Long Mesa fire burned at least three distinct vegetation types (mountain shrublands, piñon-juniper woodlands, and Douglas fir forests) and covered a mosaic of previously burned patches. The major controlling factor is prefire vegetation structure, which influences the predominant fire behavior via the nature of the fuels complex, and controls the kinds of plant responses that can occur. The previous fire history influences post-fire patterns to a lesser degree. In addition to the community-level heterogeneity of responses that we found in the burned woodlands and shrublands of MVNP, a rich variety of individual species responses to fire occurred. Conifer recovery is not yet evident after 8 years. The spatial extent of non-native plant species was mapped within the burn and compared with the non-native plant distribution in 1993.

Introduction

The role of fire in the long-term development of piñon-juniper woodlands and mountain shrublands of western North America is poorly understood. In southwestern Colorado and throughout the western slope of the southern Rocky Mountains, extensive piñon-juniper, *Pinus edulis* Engelm.-*Juniperus osteosperma* Sarg., stands interdigitate with dense mountain shrub communities or "Petran" chaparral (Keeley and Keeley, 1988). *Quercus gambelii* (Gambel or scrub oak), *Amelanchier utahensis* (Utah serviceberry), *Peraphyllum ramossisum* (squaw apple) and *Fendlera rupicola* (Fendler bush) form tall shrub thickets in the Petran, while *Artemisia nova* (black sagebrush), and *Purshia tridentata* (bitterbrush) form low shrub communities. We are investigating fire's influence in these ecosystems, both in terms of post-fire succession and fire history. Here, we report on the initial 8 years of post-fire succession following the 1989 Long Mesa fire in Mesa Verde National Park, located in Southwestern Colorado, USA (Figure 1).

On July 8, 1989, lightning struck the middle elevation of Long Mesa on the western end of Mesa Verde National Park. The two week burn covered 1200 hectares of both mesa-top and canyon terrain, at elevations between 2180 and 2517 m. Pre-fire vegetation on Long Mesa was a mosaic of mature piñon-juniper woodlands and mountain shrub associations which had

regenerated after fires in the 1860's (Floyd-Hanna and Romme, 1995), in the 1870's (Erdman, 1970), in 1899, in 1934, and in 1972 (unpublished Park records

Reproductive strategies of species in the PJ ecosystem: Colorado piñon pine, *Pinus edulis*, seeds are not available each year to contribute to post-fire successional plant communities. Rather this species produces "mast" crops at irregular intervals, often from 4 and 7 years, resulting in erratic recruitment (Floyd, 1986). Piñon seedlings require shade and temperature amelioration by "nurse" species such as shrubs or mature trees (Everett, et al., 1986). Utah Juniper seeds are available annually, however the size of the seed crop can vary tremendously from year to year. Gambel oak and Utah serviceberry dominate Mesa Verde's shrublands, and although they appear to provide the microhabitat qualities required of conifer seedlings in other areas (Floyd, 1982), our observations suggest that few piñon and juniper seedlings are invading the mountain shrub communities in Mesa Verde.

Shrub species may be classified "seeders," which succumb to fire and must re-establish from seed, and "sprouters" whose below-ground structures survive fires and produce new stems. This distinction provides a variety of possibilities for shrub species to enter the post-fire successional process (Fischer and Bradley, 1987). Post-fire recovery, particularly with regard to these alternate strategies, varies with the intensity of fire and the type of pre-fire vegetation. Resprouter species in Mesa Verde N.P. include *Quercus gambelii*, *Amelanchier utahensis*, *Rhus trilobata*, and *Symphoricarpos oreophilus*. Obligate seeder species include *Purshia tridentata*, *Artemisia tridentata*, and *A. nova* (Noste and Bushey, 1987). Rowe (1983) proposes an alternative classification of post-fire recovery strategies. His terminology includes "invader," "resister," "endurers" and "avoider" shrubs. Our work suggests that the descriptive classification of Fischer and Bradley (1987) best fits the patterns seen at MVNP.

Scope of this report: Following the Long Mesa Fire, the National Park Service funded a research project in which the patterns in post-fire recovery were studied at 2, 3 and 5 year intervals after the burn (Floyd-Hanna and Romme, 1995). The current study was an extension of this original work, but was very limited in scope and funding.

- We surveyed a subset of the original sampling points on Long Mesa to determine general patterns in post-fire recovery.
- We searched for threatened, endangered, and sensitive plant species.
- We outlined the spatial extent of the noxious weeds in the burn.

We report on the general patterns of post-fire succession during the first 8 years following the 1989 Long Mesa Fire. We will then discuss possible post-fire successional pathways based on more thorough sampling in past years (Floyd-Hanna and Romme, reports on file).

Methods

Description of the study area: Mesa Verde National Park is located in southwestern Colorado, USA, near the "Four Corners" intersection of the states Utah, Colorado, New Mexico and Arizona. Mesa Verde lies in a region transitional between the Colorado Plateau and the southern Rocky Mountains. This is exemplified by the range of vegetation communities found here, including extensive piñon-juniper forests at lower elevations characteristic of the Colorado Plateau to Douglas Fir forests characteristic of the neighboring mountains at the upper elevations. Extensive mountain shrubland, or Petran chaparral, and isolated stands of Ponderosa Pine (*Pinus ponderosa*) are also supported. The mesa is composed of high, gently sloping terrain cut by deep canyons spanning elevations between 1850 m and 2650 m. The geologic substrate consists of Mancos shale capped by the resistant Cliffhouse Sandstone. Between these formations lie the Point Lookout Sandstones and the Menefee shales (Griffitts, 1991). Due to the gentle southerly dip of these beds, the older Point Lookout sandstones are exposed at the highest elevations, while the younger Menefee and Cliffhouse formations form the deep canyons and spectacular alcoves in the lower reaches of the mesa. Annual precipitation on the Mesa averages approximately 30-40 cm. Most of this occurs as winter precipitation in the form of snow and during the summer monsoons as thundershowers. This study was conducted within Mesa Verde National Park which comprise approximately 26 000 ha on the mesa between UTM zone 12 coordinates, 716,720 and 736,310 east, 4114670 and 4136750 north.

Description of the complete post-fire succession study (1991-1998): Three sampling grids were established in 1991 to include the range of pre-fire vegetation on Long Mesa, within Long Canyon, and on the north escarpment of Mesa Verde National Park, MVNP, (Figure 1).

1. Long Mesa Southern Grid (# 1): This grid consists of a square kilometer, sampled systematically every 100 meters, for a total of 121 sampling points. It was chosen to represent the heterogeneity of vegetation within the piñon-juniper/shrubland mosaic that characterizes mid elevations in MVNP. This sampling grid also spans Long Mesa and Long Canyon. "Control points" consisted of vegetation missed by the 1989 fire, but burned in earlier fires.
2. Long Mesa Northern Grid (# 2): The second grid was placed within the essentially treeless, mountain shrub community which extends over much of the northern and slightly higher sector of the Park. As the vegetation was relatively homogenous, the size was reduced to 1 km by 0.6 km, and the number of sampling points to 66.
3. North Escarpment Grid (# 3): The Long Mesa fire jumped over the North Escarpment, and ran in strips down toward the base of this steep slope. The terrain was very difficult to sample, so the grid placement and sampling structure was modified for safety of the personnel. Grid # 3 covers the Douglas-Fir/shrubland association which is of limited distribution on north-facing slopes. The grid ran 0.5 km in length and 0.4 km in width, and samples points were placed every 50 m.

Data were collected in the summer of 1991, 1992, and 1994 on each grid point. In 1997, a subset of 32 points were sampled in Grid #1 and 2 due to limited funding. At each point the percent cover of living plants, unburned litter, burned litter, bare mineral soil, and rock substrates were sampled within four 0.25 m² quadrats. The quadrats were located along a 4-m line centered on the sampling point. Sampling was by means of the point-intercept method (Mueller-Dombois and Ellenburg, 1974). The sampling frame (modified from one designed by Floyd and Anderson, 1982) was placed 4 times (at 1 or 3 m either side of sampling point) and the vegetation or substrate intersected by 2 sets of crossed strings were recorded. Alternating with the placement of the sample quadrat, we excavated a shallow hole with a knife and measured the depth of soil char in the first year of sampling. The dominant grasses and forbs were recorded, and the number of burned and unburned stems of shrubs and trees were counted. Rock spalling and oxidation of sandstones were noted as indicators of relative fire intensity. Site characteristics such as slope, aspect, soil and geology were recorded. The frequency of each variable was transformed with an arcsin transformation (arcsin of the square root of the raw frequency since data of this kind are not normally distributed without transformation) (Sokal and Rolf, 1987).

For simplicity, the arcsin of the frequency of encounters with each variable will be denoted as its cover in capitals, e.g. FORB represents the arcsin transformation of the frequency of data points intersecting forbs of any species. FORBS, grasses (GRASS), bare soils (BARESOIL), litter (LITTER), charred litter (CHARLITTER), live and dead shrubs (LIVESHURUB or DEADSHURUB), and mosses (MOSESSES) were recorded.

Each variable was summarized in 1997 to determine trends in that variable during 8 years of post-fire succession. A series of two-way analysis of variance (ANOVA) were carried out on each variable to determine whether the variation in cover could be explained by either pre-fire vegetation or the previous fire history (Appendix A). Pre-fire vegetation includes (a) piñon-juniper woodland, with minimal shrub component (b) piñon-juniper/shrubland, consisting of sparse trees within a dense stand of oak (c) shrubland—primarily Gambel oak and Utah serviceberry, (d) sagebrush—primarily black sage and bitterbrush, and (e) Douglas fir/shrubland. Fire history was identified as (a) unburned since at least 1940 ("control"), (b) burned in 1972, (c) burned in 1989 and (d) areas which burned in both 1972 and 1989. It is likely that many of these sampling points also burned in the 1860's, 1870's, 1899, and 1934 fires as well, but the spatial extent of these earlier fires was not known precisely enough to include them in the ANOVA.

In August, 1997, a Prescott College class used GPS technology to outline the periphery of the major weedy species in the Long Mesa burn. This was overlain on a topographic image of the Long Mesa and Wetherill Mesa area and the spatial extent of polygons containing weeds were calculated in Arc-Info software (Figure 3 and report on file with Resource Management). A base map outlining the weed distribution was produced by a pedestrian survey in 1993 (Figure 2), and serves as an excellent comparison of the weed expansion over the 5 intervening years.

Results

The cover of each type of plant— grass, forb shrub, etc— is averaged in Figure 4 for all the sampled points combined, then in Figure 5 for the piñon-juniper sampling points and in Figure 6 for the shrub sampling points.

Appendix A summarizes the Analysis of Variance tests of the 1997. We test whether there is a significant difference among each plant structural type (i.e. forb, grass, liveshrub, etc) of varying pre-fire vegetation and the fire history

There was no difference in the bare soil exposure across all fire histories and pre-fire vegetation communities. There was a significantly greater forb cover in sampling areas which burned in the 1989 fire than those which burned in the 1972, 1972/1989 and the 1934 fires. Grasses were also significantly greater in the 1989 sample points. Live shrub cover was greatest in the 1972 burned sampling points.

Threatened and Endangered Plant Species

In July, 1998, we found a robust population of *Hackelia gracilentia* persisting in Long Canyon on the west-facing side of Long Canyon, near the Long Mesa trail. While it had been present during the first 2 years after the fire, there is now no evidence of *Nicotiana attenuata* in the Long Mesa fire.

Biological invasions

A comparison of the distribution of weedy populations in Figures 2 and 3 indicates that at least some species have expanded their range considerably. However, a direct comparison is difficult to make, as new species came into Long Mesa between 1993 and 1997. We have tried to focus on Musk and Canada thistles. Please see the report on file in Resource Management Office, Mesa Verde National Park, by Floyd-Hanna, Hanna and Prescott College Students, 1997 for details.

Discussion

In the 1960s Erdman (1970) made a pioneering study of postfire succession in Mesa Verde National Park which has been frequently cited as a key reference on fire effects and plant responses in this system. Based on sampling a chronosequence of burned sites, including one recently burned area, Erdman described a single successional trajectory moving through an annual-dominated stage, a perennial grass and forb stage, a shrub stage, and finally the mature piñon-juniper woodland. In the light of our more extensive sampling of the Long Mesa burn, and our explicit focus on the heterogeneity of fire effects and responses, we can now expand Erdman's model into a more comprehensive picture of post-fire succession in Mesa Verde. It is apparent from our results that Erdman's initial annual plant stage is manifested only in certain situations, e.g., where a piñon-juniper woodland burns at high intensity with heavy mortality of trees, shrubs, and herbs, and the exposure of much bare soil where annuals can become established. Where shrublands burn at lower intensity, the surviving below ground parts of the dominant shrubs re-sprout so quickly and

so prolifically that they reestablish dominance before annuals can invade the site in substantial numbers. In these latter areas there is no annual stage, nor even a grass - forb stage; rather the pre-fire shrub community becomes reestablished promptly with no "succession" being apparent. Since at least some of the mountain shrublands in MVNP are successional stages leading to piñon-juniper woodlands, these findings indicate fundamentally different successional trajectories following fire that occurs in early or mid successional stages versus fire in late successional stages, within the same general environment and vegetation type.

Thus, we find support for our hypothesis of multiple pathways of succession in Mesa Verde National Park. Three major kinds of successional trajectories during the first 8 years after fire are summarized in Table 1. The major controlling factor in this model is pre-fire vegetation structure, which influences the predominant fire behavior (via the nature of the fuels complex), and the kinds of plant responses that can occur. The vegetation over much of Mesa Verde is a mosaic of these three types of community structure, and hence the effects of fire and the early post-fire succession patterns also appear as a heterogeneous mosaic rather than a single uniform successional stage.

The model depicted in Table 1 demonstrates how structurally different kinds of plant communities will exhibit different kinds of postfire responses. Also of interest to the fundamental theoretical question of multiple successional pathways (e.g., Glenn-Lewin and van der Maarel 1992) is the comparison of areas in Mesa Verde that had similar pre-fire structure (i.e., shrublands) but different histories before the fire of 1989 (i.e., sites that burned twice within a short period of time, in 1972 and again in 1989, in contrast with sites that had not burned for many decades prior to the fire in 1989). Two years after the 1989 fire, we found lower cover of live shrubs and forbs, and higher cover of bare ground, in the areas that had burned twice compared to those that had burned only once. This difference in live shrubs and bare ground persisted through at least the fifth year after the fire, supporting the idea that succession was at least somewhat different in these areas of different fire history. In particular, repeated burning at short intervals would appear to reduce shrub vigor and shrub dominance. Elsewhere in the southwest, a second burning within a short interval reduced the biomass of Gambel oak by 12-20 % when compared with single burn experiments (Harrington, 1985). Carbohydrate depletion in underground reserves may account for these observations. Interestingly, the difference in forb cover that we detected in our study area between once and twice burned sites did not persist beyond the second year after the fire. On the contrary, the twice-burned sites had higher forb cover in years 3 and 5. Unfortunately, our sampling methods did not include detailed floristic information, so we do not know how species composition may have changed between years and sites. However, we hypothesize that the greater increase in forb cover on the twice-burned sites represents a greater establishment of new species from outside the burn because of reduced competition from resprouting plants and greater availability of bare soil.

Another interesting difference in early postfire communities, where prefire vegetation structure was similar, can be seen by comparing those areas where exotic weeds (*Carduus nutans*, *Cirsium arvense*, *Bromus tectorum*, and others) invaded after the fire with areas where the weeds did not become

established. Of the entire Long Mesa burn, 7.5 % was infested with *Carduus nutans* (muskthistle) by 1993 (Floyd-Hanna et al. 1993) but the populations expanded considerably by 1997 (see report on file with Resource Management).

However, serious weed invasion of burned areas has occurred only in some of the former piñon-juniper woodlands; other severely burned woodlands and nearly all burned shrublands now support very few weeds. Which piñon-juniper sites were invaded and which were not appears to have been largely a matter of chance: those areas that happened to be in close proximity to a seed source were invaded. Seed sources usually were areas of disturbed soil that supported a few weeds before the fire, such as roads, trails, and small patches of piñon recently killed by a root fungus (*Verticicladiella wagnerii*).

It also happened that several years after the fire were marked by an unusually long and moist growing season – conditions that especially favor the growth of *Carduus nutans*. Thus there is another stochastic element related to weather condition in the early years of post-fire succession. Where the exotic weeds now dominate stands, they appear to be competitively excluding the native plants that are abundant in other areas that lack the weeds. This suggests that long-term successional trajectories may be substantially different between burned piñon-juniper woodlands that have been invaded by weeds and those that have not. Persistent stands of exotic thistles occur in numerous sites near Mesa Verde throughout La Plata and Montezuma counties, Colorado, and have expanded rapidly since their initial invasion during the 1970's. Although disturbance appears necessary for large-scale muskthistle invasion, patches of muskthistle also can be in openings of mature piñon-juniper woodlands as well as in larger disturbed sites. Biological invasion of Mesa Verde National Park on disturbed habitats illustrates the complexity of problems created by species migration and the role of human effects on plant succession.

Conclusions

Post-fire succession following the Long Mesa Burn, in Mesa Verde National Park, southwestern Colorado, USA was studied from 1991-1994 and followed by limited sampling in the area in 1997. Early successional patterns varied with previous vegetation and fire history of the sampling site. Perennial shrub resprouting preempted forb and grass communities in burned mountain shrublands; after five years, seed-producing shrub species such as sagebrush and bitterbrush were gaining importance. Multiple pathways of succession are evident throughout the Long Mesa burn. and several major successional trajectories during the first 8 years after fire are summarized. The major controlling factor in this model is prefire vegetation structure, which influences the predominant fire behavior and patterns of plant response to fire.

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Table 1 Fire effects and successional trajectories in three major pre-fire vegetation types in Mesa Verde National Park, Colorado, U.S.A.

	Piñon-Juniper Woodlands	Oak-Serviceberry Shrublands	Black Sagebrush - Grasslands
Dominant Species before the Fire	small trees (<i>Pinus edulis</i> , <i>Juniperus osteosperma</i>); low to tall shrubs (<i>Purshia tridentata</i> , <i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>); herbs (<i>Lupinus caudatus</i>); grasses (<i>Poa fendleriana</i>)	tall shrubs (<i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>); herbs (<i>Wyethia arizonica</i>); grasses (<i>Poa pratense</i> , <i>Oryzopsis hymenoides</i>)	low shrubs (<i>Artemisia nova</i> , <i>Purshia tridentata</i>); herbs (<i>Lupinus ammophilus</i> , <i>Viguera multiflora</i>); grasses (<i>Stipa comata</i> , <i>Sitanion hystrix</i>)
Predominant Fire Behavior in large fires	long duration of burning in heavy fuels, with high to very high heat release	brief duration of burning in light to moderate fuels, with moderate to high heat release	brief duration of burning in light fuels, with low to moderate heat release
Initial Fire Effects	high mortality of trees, shrubs, and perennial herbs; complete consumption of litter and live foliage; much bare soil exposed, very little litter	aboveground mortality of shrubs and herbs but survival of belowground structures; consumption of litter but not of live foliage; moderate bare soil exposed, moderate amount of litter from fall of scorched leaves	high mortality of shrubs; aboveground but not belowground mortality of perennial herbs; consumption of litter and live foliage; moderate bare soil exposed, little litter
Plant Responses	trees reestablish very slowly (decades or centuries) by seed from sources outside burned area; some sprouting of shrubs and herbs; rapid and prolonged establishment of opportunistic species (including weeds) by seed from outside burned area	prolific resprouting of shrubs and herbs, with very rapid (2 yr) reestablishment of pre-fire cover; little establishment of opportunistic species by seed because of competition from established plants and lack of bare soil	moderately rapid (5 yr) establishment of shrubs by seed from outside burned area; rapid resprouting of perennial herbs; brief early establishment of a few opportunistic species by seed from outside burned area
Community Structure after 5 Years	no living trees but many standing and fallen snags; moderate cover of resprouting shrubs and herbs; moderate to high cover of opportunistic species including weeds	high cover of resprouting shrubs and perennial herbs; composition and structure similar to pre-fire stands; low cover of opportunistic species	low shrub cover; high cover of resprouting perennial herbs; low to moderate cover of opportunistic species

Figure 1:

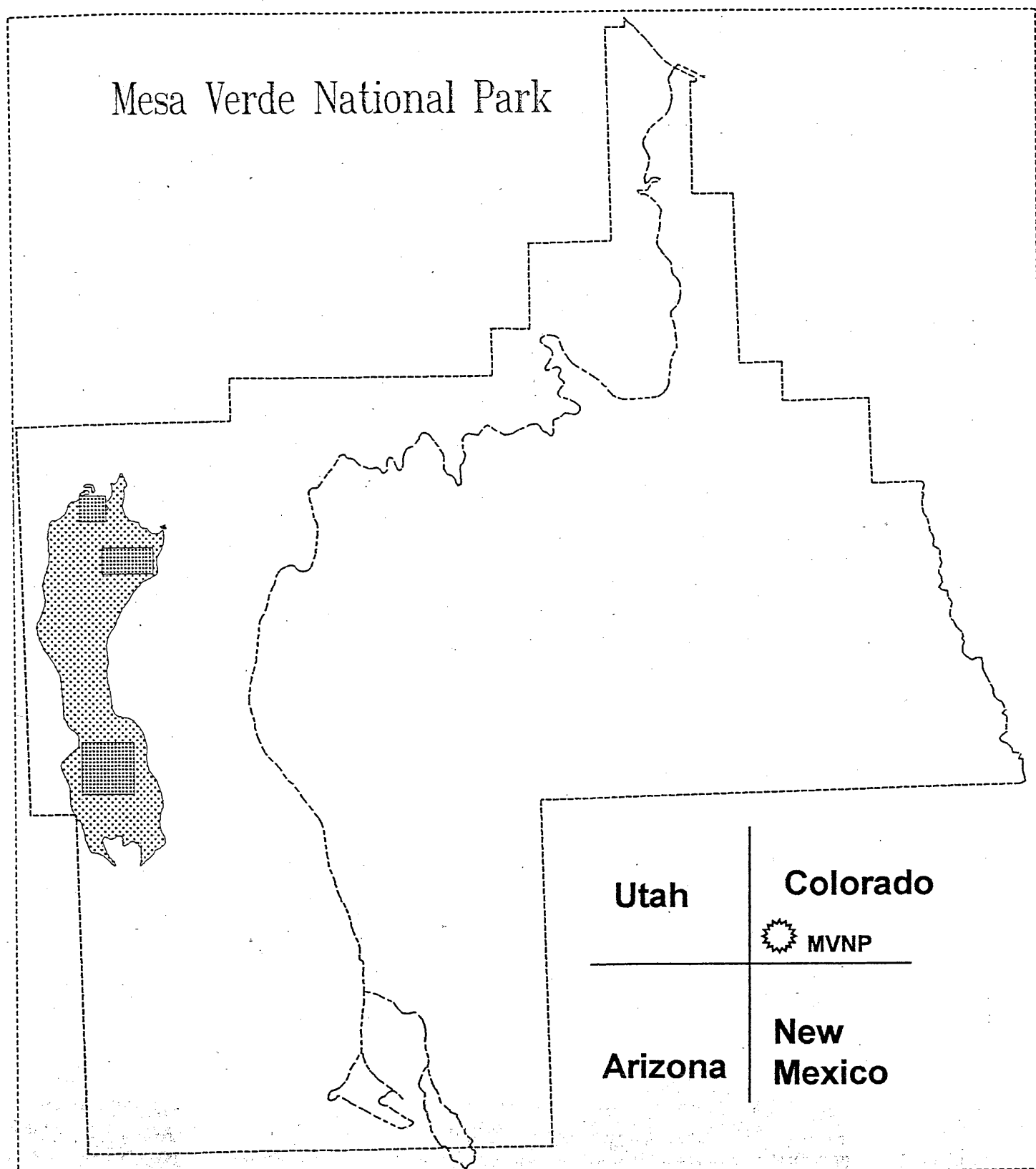
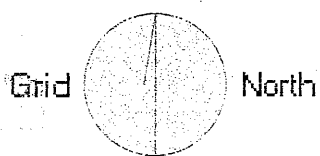
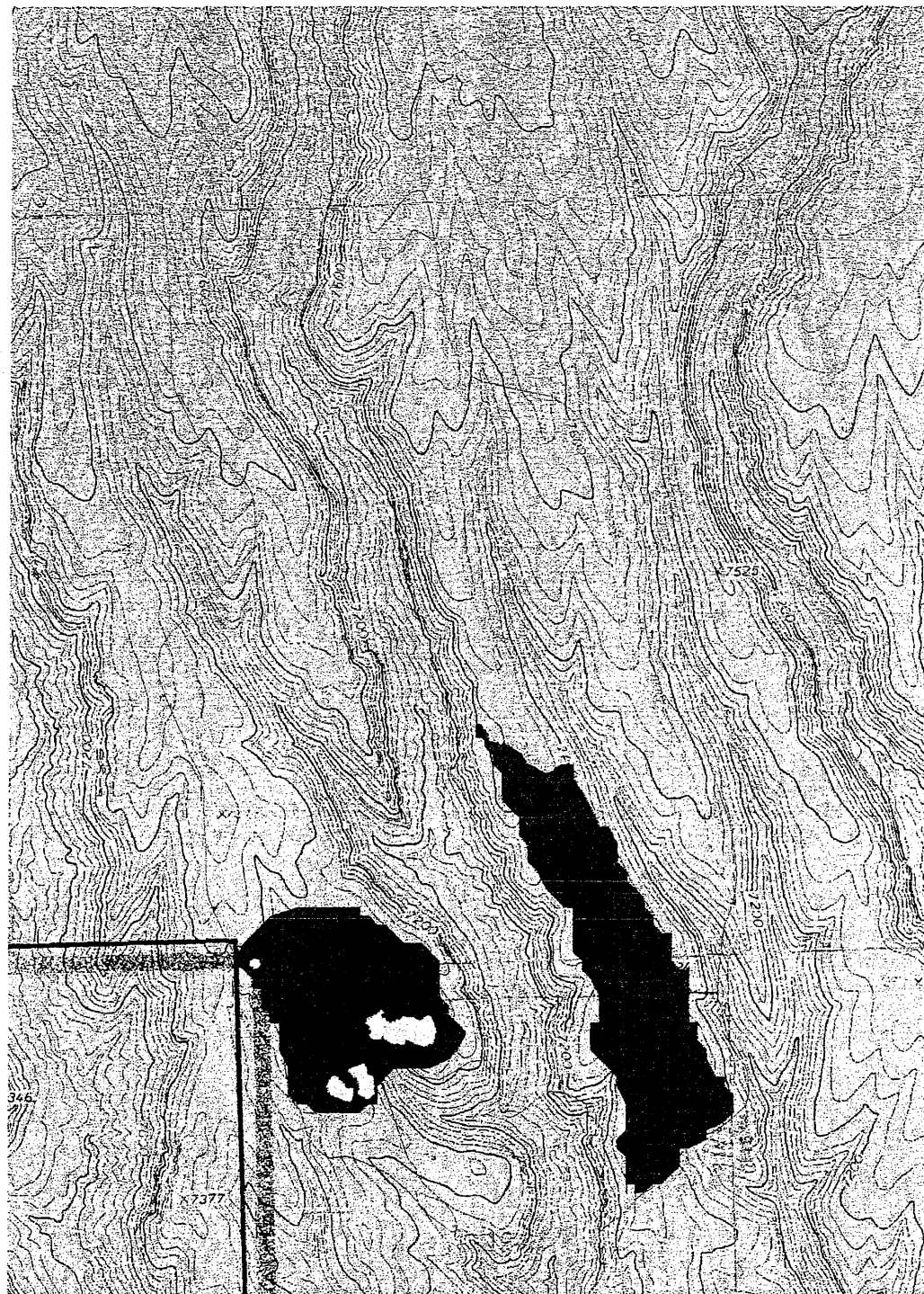


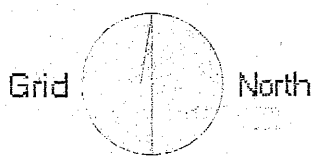
Figure 2. Extent of Weeds on Long Mesa, 1993



Meters
1000.00

Figure 2. The spatial distribution of non-native plant species in 1993 within the Long Mesa Fire, Mesa Verde National Park, Colorado.

Figure 3. Extent of Weeds on Long Mesa, 1997



Meters
1000.00

Figure 3. The spatial distribution of non-native plant species in 1997 within the Long Mesa Fire, Mesa Verde National Park, Colorado. The colors represent specific densities of weeds: Blue= sparse, yellow=patchy, red=dense, green=extremely dense.

The Recovery of Vegetation after 8 Years Long Mesa Fire, Mesa Verde National Park

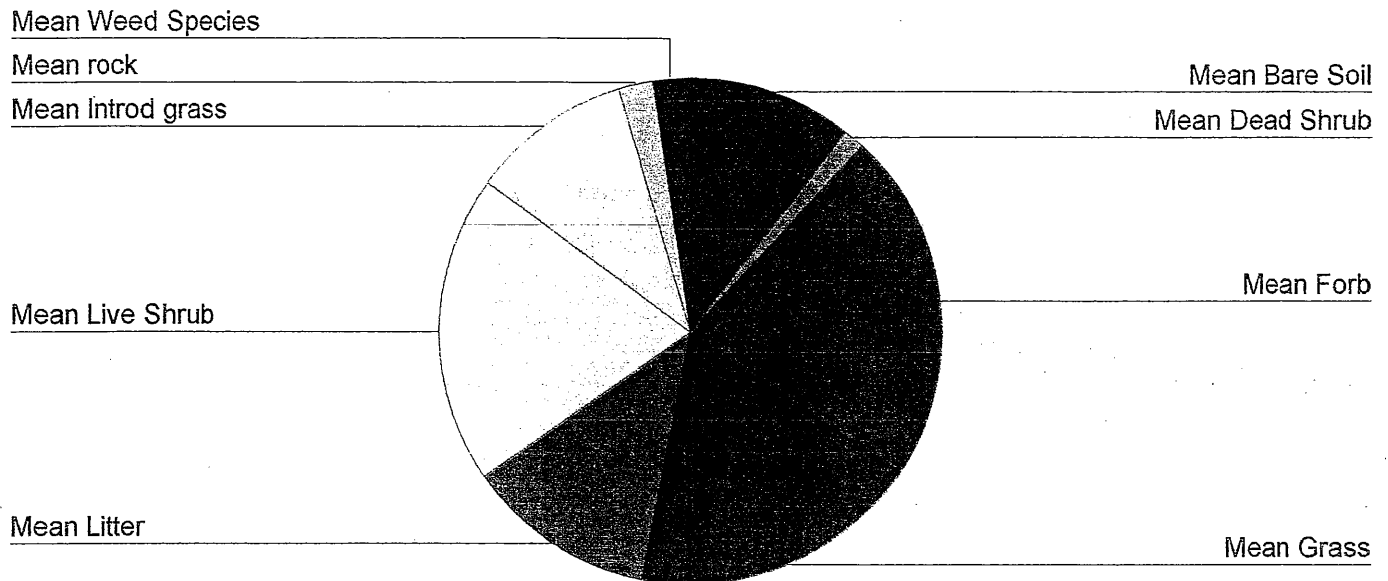


Figure 4. The mean cover of each type of plant growing at selected sampling points in the Long Mesa Fire, Mesa Verde National Park.

The Recovery of Vegetation after 8 Years Shrubland Grid, Long Mesa

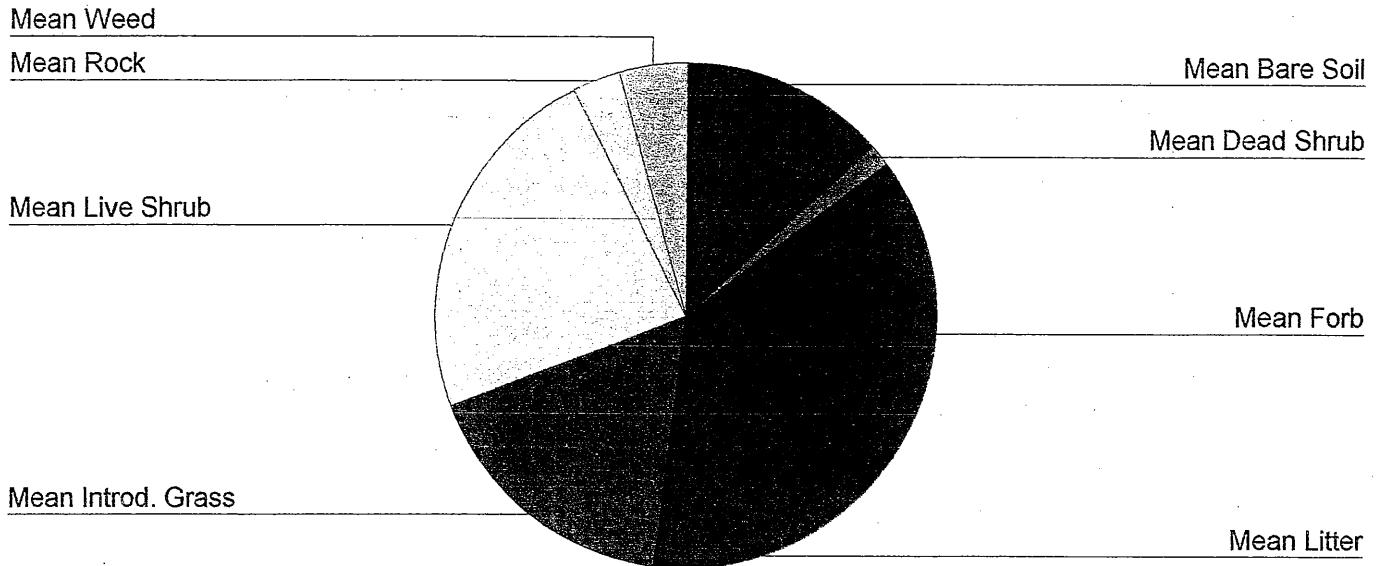


Figure 5. The mean cover of each type of plant growing at selected sampling points within the pinon-juniper portion of the Long Mesa Fire, Mesa Verde National Park.

The Recovery of Vegetation after 8 years Lower Pinon Juniper Grid, Long Mesa

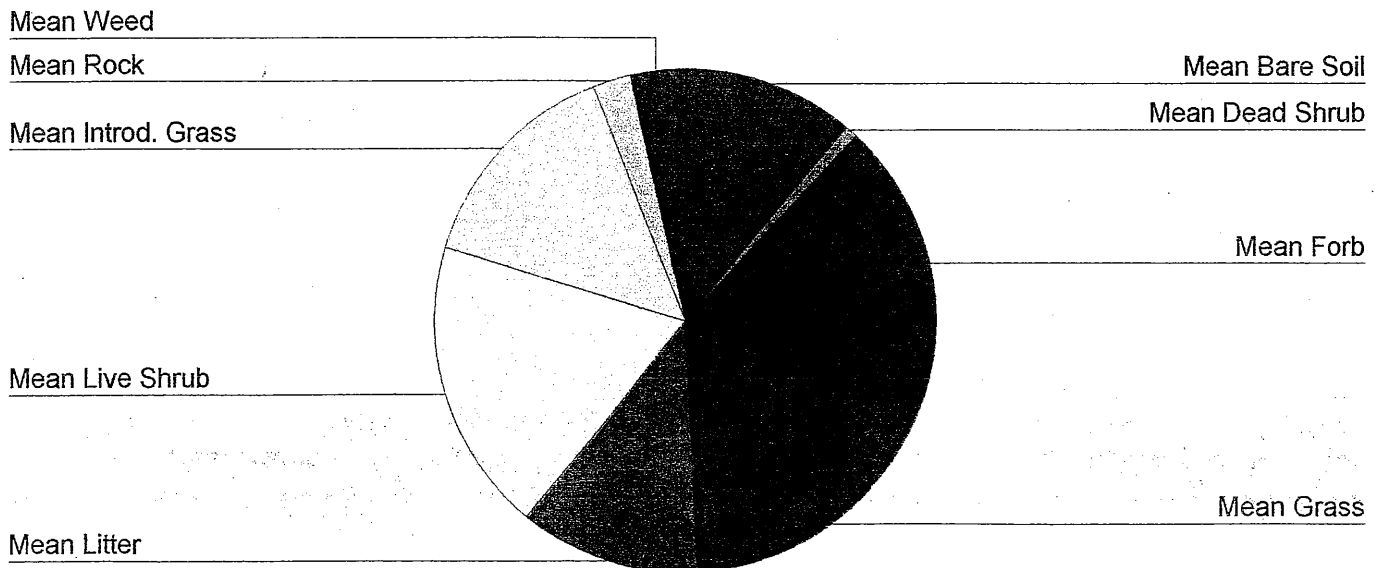


Figure 6. The mean cover of each type of plant growing at selected sampling points within the shrubland portion of the Long Mesa Fire, Mesa Verde National Park.

Appendix A

29 Mar 98- ANOVA of 1998 Long Mesa Data, post-fire structural responses by vegetation category across pre-fire vegetation and various fire histories. Floyd-Hanna

* * * C E L L M E A N S * * *

ARCBAR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.13
(128)

FIREHIST

pre 1990

1959

1972

1989

72/89

1

2

3

4

.17 .00 .15 .12 .00
(18) (0) (8) (102) (0)

PRE_FIRE

1 mtn shrubs

ps 2

35 shrubs

4 sage

1

2

3

4

.03 .14 .13 .00
(4) (50) (74) (0)

PRE_FIRE

1

2

3

4

FIREHIST

0 .00 .13 .18 .00
(0) (3) (15) (0)

1 .00 .00 .00 .00
(0) (0) (0) (0)

2 .00 .08 .22 .00
(0) (4) (4) (0)

3 .03 .15 .11 .00
(4) (43) (55) (0)

4 .00 .00 .00 .00
(0) (0) (0) (0)

* * * A N A L Y S I S O F V A R I A N C E * * *

ARCBAR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.096	4	.024	.785	.537
FIREHIST	.045	2	.023	.747	.476
PRE_FIRE	.050	2	.025	.823	.442
2-Way Interactions	.076	2	.038	1.257	.288
FIREHIST PRE_FIRE	.076	2	.038	1.257	.288
Explained	.172	6	.029	.942	.468
Residual	3.682	121	.030		

* * * C E L L M E A N S * * *

ARCDSH97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.02
(120)

FIREHIST	0	1	2	3	4
	.02	.00	.01	.02	.00
(15)	(0)	(5)	(100)	(0)	

PRE_FIRE	1	2	3	4
	.00	.02	.02	.00
(4)	(45)	(71)	(0)	

		PRE_FIRE			
		1	2	3	4
FIREHIST	0	.00	.16	.01	.00
	(0)	(1)	(14)	(0)	
	1	.00	.00	.00	.00
	(0)	(0)	(0)	(0)	
	2	.00	.00	.04	.00
	(0)	(4)	(1)	(0)	
	3	.00	.01	.02	.00
	(4)	(40)	(56)	(0)	
	4	.00	.00	.00	.00
	(0)	(0)	(0)	(0)	

* * * A N A L Y S I S O F V A R I A N C E * * *

ARCDSH97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.002	4	.000	.216	.929
FIREHIST	.001	2	.000	.184	.832
PRE_FIRE	.001	2	.001	.247	.781
2-Way Interactions	.022	2	.011	5.360	.006
FIREHIST PRE_FIRE	.022	2	.011	5.360	.006
Explained	.024	6	.004	1.931	.082
Residual	.236	113	.002		
Total	.260	119	.002		

* * * C E L L M E A N S * * *

ARCFOR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.24
(128)

FIREHIST	0	1	2	3	4
	.10	.00	.18	.27	.00
(18)	(0)	(6)	(104)	(0)	

PRE_FIRE	1	2	3	4
	.26	.24	.25	.00
(4)	(50)	(74)	(0)	

	PRE_FIRE				
	1	2	3	4	
FIREHIST	0	.00	.08	.11	.00
	(0)	(2)	(16)	(0)	
	1	.00	.00	.00	.00
	(0)	(0)	(0)	(0)	
	2	.00	.15	.25	.00
	(0)	(4)	(2)	(0)	
	3	.26	.25	.29	.00
	(4)	(44)	(56)	(0)	
	4	.00	.00	.00	.00
	(0)	(0)	(0)	(0)	

* * * A N A L Y S I S O F V A R I A N C E * * *

ARCFOR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.499	4	.125	1.776	.138
FIREHIST	.458	2	.229	3.260	.042
PRE_FIRE	.041	2	.020	.292	.747
2-Way Interactions	.004	2	.002	.031	.969
FIREHIST PRE_FIRE	.004	2	.002	.031	.969
Explained	.503	6	.084	1.194	.314
Residual	8.490	121	.070		
Total	8.993	127	.071		

* * * C E L L M E A N S * * *

ARCGR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.21
(128)

FIREHIST					
0	1	2	3	4	
.10	.00	.12	.23	.00	
(17)	(0)	(7)	(104)	(0)	

PRE_FIRE				
1	2	3	4	
.46	.21	.19	.00	
(4)	(51)	(73)	(0)	

	PRE_FIRE				
	1	2	3	4	
FIREHIST					
0	.00	.28	.06	.00	
	(0)	(3)	(14)	(0)	
1	.00	.00	.00	.00	
	(0)	(0)	(0)	(0)	
2	.00	.01	.27	.00	
	(0)	(4)	(3)	(0)	
3	.46	.22	.22	.00	
	(4)	(44)	(56)	(0)	
4	.00	.00	.00	.00	
	(0)	(0)	(0)	(0)	

* * * A N A L Y S I S O F V A R I A N C E * * *

ARCGR97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.527	4	.132	2.550	.043
FIREHIST	.310	2	.155	3.005	.053
PRE_FIRE	.216	2	.108	2.094	.128
2-Way Interactions	.247	2	.123	2.390	.096
FIREHIST PRE_FIRE	.247	2	.123	2.390	.096
Explained	.774	6	.129	2.496	.026
Residual	6.250	121	.052		
Total	7.024	127	.055		

ARCLIT97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.13
(127)

FIREHIST	0	1	2	3	4
	.17 (19)	.00 (0)	.07 (6)	.12 (102)	.00 (0)

PRE_FIRE	1	2	3	4
	.00 (4)	.13 (50)	.14 (73)	.00 (0)

	PRE_FIRE			
	1	2	3	4
FIREHIST 0	.00 (0)	.15 (3)	.17 (16)	.00 (0)
1	.00 (0)	.00 (0)	.00 (0)	.00 (0)
2	.00 (0)	.06 (4)	.10 (2)	.00 (0)
3	.00 (4)	.13 (43)	.13 (55)	.00 (0)
4	.00 (0)	.00 (0)	.00 (0)	.00 (0)

*** ANALYSIS OF VARIANCE ***

ARCLIT97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.113	4	.028	1.353	.254
FIREHIST	.048	2	.024	1.144	.322
PRE_FIRE	.065	2	.033	1.562	.214
2-Way Interactions	.005	2	.002	.117	.890
FIREHIST PRE_FIRE	.005	2	.002	.117	.890
Explained	.118	6	.020	.941	.468
Residual	2.501	120	.021		
Total	2.618	126	.021		

ARCLS97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

Total Population

.28
(125)

FIREHIST	0	1	2	3	4
	.38	.00	1.19	.17	.00
(17)	(0)	(9)	(99)	(0)	

PRE_FIRE	1	2	3	4
	.14	.23	.31	.00
(4)	(46)	(75)	(0)	

	PRE_FIRE			
	1	2	3	4
FIREHIST				
0	.00	.46	.37	.00
(0)	(2)	(15)	(0)	
1	.00	.00	.00	.00
(0)	(0)	(0)	(0)	
2	.00	.93	1.40	.00
(0)	(4)	(5)	(0)	
3	.14	.15	.19	.00
(4)	(40)	(55)	(0)	
4	.00	.00	.00	.00
(0)	(0)	(0)	(0)	

* * * ANALYSIS OF VARIANCE * * *

ARCLS97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	8.839	4	2.210	12.778	.000
FIREHIST	8.707	2	4.353	25.175	.000
PRE_FIRE	.132	2	.066	.381	.684
2-Way Interactions	.404	2	.202	1.167	.315
FIREHIST PRE_FIRE	.404	2	.202	1.167	.315
Explained	9.243	6	1.540	8.908	.000
Residual	20.406	118	.173		
Total	29.648	124	.239		

* * * CELL MEANS * * *

ARCNG97
by FIREHIST FIRE HISTORY

PRE_FIRE PRE-FIRE VEGETATION

Total Population

.12
(124)

FIREHIST

	0	1	2	3	4
	.16	.00	.18	.11	.00
(	14)	(0)	(8)	(102)	(0)

PRE_FIRE

	1	2	3	4
	.22	.12	.11	.00
(	4)	(47)	(73)	(0)

		PRE_FIRE			
		1	2	3	4
FIREHIST	0	.00	.00	.16	.00
	(	0)	(0)	(14)	(0)
	1	.00	.00	.00	.00
	(	0)	(0)	(0)	(0)
	2	.00	.05	.31	.00
(	0)	(4)	(4)	(0)	
3	.22	.13	.08	.00	
(	4)	(43)	(55)	(0)	
4	.00	.00	.00	.00	
(	0)	(0)	(0)	(0)	

* * * ANALYSIS OF VARIANCE * * *

ARCNG97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.123	4	.031	.644	.633
FIREHIST	.063	2	.031	.657	.521
PRE_FIRE	.060	2	.030	.630	.534
2-Way Interactions	.164	1	.164	3.436	.066
FIREHIST PRE_FIRE	.164	1	.164	3.436	.066
Explained	.286	5	.057	1.202	.312
Residual	5.618	118	.048		
Total	5.905	123	.048		

* * * CELL MEANS * * *

ARCWE97
by FIREHIST FIRE HISTORY

Total Population

.03
(117)

FIREHIST

	0	1	2	3	4
	.08	.00	.01	.03	.00
(15)	(0)	(4)	(98)	(0)	

PRE_FIRE

	1	2	3	4
	.00	.02	.04	.00
(4)	(44)	(69)	(0)	

	PRE_FIRE			
	1	2	3	4
FIREHIST 0	.00 (0)	.00 (0)	.08 (15)	.00 (0)
1	.00 (0)	.00 (0)	.00 (0)	.00 (0)
2	.00 (0)	.01 (4)	.00 (0)	.00 (0)
3	.00 (4)	.02 (40)	.03 (54)	.00 (0)
4	.00 (0)	.00 (0)	.00 (0)	.00 (0)

* * * ANALYSIS OF VARIANCE * * *

ARCWE97
by FIREHIST FIRE HISTORY
PRE_FIRE PRE-FIRE VEGETATION

HIERARCHICAL sums of squares
Covariates entered FIRST

Source of Variation	Sum of Squares	DF	Mean Square	F	Sig of F
Main Effects	.040	4	.010	1.185	.321
FIREHIST	.034	2	.017	2.015	.138
PRE_FIRE	.006	2	.003	.355	.702
Explained	.040	4	.010	1.185	.321
Residual	.954	112	.009		
Total	.994	116	.009		

COMPARISON OF THE COVER OF EACH PLANT TYPE ACROSS UPPER AND LOWER GRIDS. UPPER GRID IS PRIMARILY SHRUBLAND AND LOWER GRID IS PRIMARILY PINON JUNIPER WOODLAND PRIOR TO THE 1989 LONG MESA FIRE.

----- O N E W A Y -----

Variable ARCBAR97
By Variable GRIDNO

Analysis of Variance

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	1	.0353	.0353	1.1749	.2804
Within Groups	128	3.8435	.0300		
Total	129	3.8788			

Group	Count	Mean	Standard Deviation	Standard Error	Minimum	Maximum	95 Pct Conf Int for Mean
Grp 1	86	.1411	.1836	.0198	.0000	.9273	.1017 TO .180
Grp 2	44	.1063	.1508	.0227	.0000	.7478	.0604 TO .152
Total	130	.1293	.1734	.0152	.0000	.9273	.0992 TO .159

----- O N E W A Y -----

Variable ARCD97
By Variable GRIDNO

Analysis of Variance

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	1	.0000	.0000	.0109	.9171
Within Groups	120	.2715	.0023		
Total	121	.2715			

Group	Count	Mean	Standard Deviation	Standard Error	Minimum	Maximum	95 Pct Conf Int for Mean
Grp 1	78	.0165	.0421	.0048	.0000	.1607	.0070 TO .0260
Grp 2	44	.0174	.0560	.0084	.0000	.2424	.0004 TO .0344
Total	122	.0168	.0474	.0043	.0000	.2424	.0083 TO .0253

----- O N E W A Y -----

Variable ARCFOR97
By Variable GRIDNO

Analysis of Variance

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	1	.1972	.1972	2.8219	.0954
Within Groups	128	8.9452	.0699		
Total	129	9.1425			

Table 6. Fire effects and successional trajectories in three major pre-fire vegetation types in Mesa Verde National Park, Colorado, U.S.A.

	Piñon-Juniper Woodlands	Oak-Serviceberry Shrublands	Black Sagebrush - Grasslands
Dominant Species before the Fire	small trees (<i>Pinus edulis</i> , <i>Juniperus osteosperma</i>); low to tall shrubs (<i>Purshia tridentata</i> , <i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>); herbs (<i>Lupinus caudatus</i>); grasses (<i>Poa fendleriana</i>)	tall shrubs (<i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>), herbs (<i>Wyethia arizonica</i>); grasses (<i>Poa pratense</i> , <i>Oryzopsis hymenoides</i>)	low shrubs (<i>Artemisia nova</i> , <i>Purshia tridentata</i>); herbs (<i>Lupinus ammophilus</i> , <i>Viguera multiflora</i>); grasses (<i>Stipa comata</i> , <i>Sitanion hystrix</i>)
Predominant Fire Behavior in large fires	long duration of burning in heavy fuels, with high to very high heat release	brief duration of burning in light to moderate fuels, with moderate to high heat release	brief duration of burning in light fuels, with low to moderate heat release
Initial Fire Effects	high mortality of trees, shrubs, and perennial herbs; complete consumption of litter and live foliage; much bare soil exposed, very little litter	aboveground mortality of shrubs and herbs but survival of belowground structures; consumption of litter but not of live foliage; moderate bare soil exposed, moderate amount of litter from fall of scorched leaves	high mortality of shrubs; aboveground but not belowground mortality of perennial herbs; consumption of litter and live foliage; moderate bare soil exposed, little litter
Plant Responses	trees reestablish very slowly (decades or centuries) by seed from sources outside burned area; some sprouting of shrubs and herbs; rapid and prolonged establishment of opportunistic species (including weeds) by seed from outside burned area	prolific resprouting of shrubs and herbs, with very rapid (2 yr) reestablishment of pre-fire cover; little establishment of opportunistic species by seed because of competition from established plants and lack of bare soil	moderately rapid (5 yr) establishment of shrubs by seed from outside burned area; rapid resprouting of perennial herbs; brief early establishment of a few opportunistic species by seed from outside burned area
Community Structure after 5 Years	no living trees but many standing and fallen snags; moderate cover of resprouting shrubs and herbs; moderate to high cover of opportunistic species including weeds	high cover of resprouting shrubs and perennial herbs; composition and structure similar to pre-fire stands; low cover of opportunistic species	low shrub cover; high cover of resprouting perennial herbs; low to moderate cover of opportunistic species

Table 7. Individualistic species responses to fire in Mesa Verde National Park, Colorado, USA.

Species	Growth Form	Predominant Fire Effect	Predominant Regeneration Mechanism	Abundance 5 Yr after Fire (relative to before fire)
<i>Pinus edulis</i>	small tree	death of entire plant	seeds, transported by birds from outside burned area (very slow)	absence of live plants
<i>Juniperus osteosperma</i>	small tree	death of entire plant	seeds, transported by birds from outside burned area (very slow)	absence of live plants
<i>Quercus gambelii</i>	tall shrub or small tree	death of aboveground stems & foliage; survival of roots	resprouting from subterranean lignotubers	cover and density equal to or greater than before fire
<i>Amelanchier utahensis</i>	tall shrub	death of aboveground stems & foliage; survival of roots	resprouting	cover and density equal to or greater than before fire
<i>Purshia tridentata</i>	low shrub	death of entire plant	seeds, dispersal mechanism unknown; rarely resprouts from roots	low cover and density
<i>Artemisia nova</i>	low shrub	death of entire plant	seeds, dispersal mechanism unknown	low cover and density
<i>Poa fendleriana</i>	bunchgrass	death of aboveground leaves & culms; roots usually unharmed	resprouting from roots, and seeds from outside burned area or from resprouting plants	cover and density equal to or greater than before the fire
<i>Lupinus caudatus</i>	perennial forb	death of aboveground leaves & stems; roots usually unharmed	resprouting from roots, and seeds produced by resprouting plants	cover and density equal to or greater than before the fire
<i>Wyethia arizonica</i>	perennial forb	death of aboveground leaves & stems; roots usually unharmed	resprouting from roots, and seeds from outside burned area or from resprouting plants	cover and density equal to or greater than before the fire

Table 1. Fire effects and successional trajectories in three major pre-fire vegetation types in Mesa Verde National Park, Colorado, U.S.A.

	Piñon-Juniper Woodlands	Oak-Serviceberry Shrublands	Black Sagebrush - Grasslands
Dominant Species before the Fire	small trees (<i>Pinus edulis</i> , <i>Juniperus osteosperma</i>); low to tall shrubs (<i>Purshia tridentata</i> , <i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>); herbs (<i>Lupinus caudatus</i>); grasses (<i>Poa fendleriana</i>)	tall shrubs (<i>Quercus gambelii</i> , <i>Amelanchier utahensis</i>), herbs (<i>Wyethia arizonica</i>); grasses (<i>Poa pratense</i> , <i>Oryzopsis hymenoides</i>)	low shrubs (<i>Artemisia nova</i> , <i>Purshia tridentata</i>); herbs (<i>Lupinus ammophilus</i> , <i>Viguera multiflora</i>); grasses (<i>Stipa comata</i> , <i>Sitanion hystrix</i>)
Predominant Fire Behavior in large fires	long duration of burning in heavy fuels, with high to very high heat release	brief duration of burning in light to moderate fuels, with moderate to high heat release	brief duration of burning in light fuels, with low to moderate heat release
Initial Fire Effects	high mortality of trees, shrubs, and perennial herbs; complete consumption of litter and live foliage; much bare soil exposed, very little litter	aboveground mortality of shrubs and herbs but survival of belowground structures; consumption of litter but not of live foliage; moderate bare soil exposed, moderate amount of litter from fall of scorched leaves	high mortality of shrubs; aboveground but not belowground mortality of perennial herbs; consumption of litter and live foliage; moderate bare soil exposed, little litter
Plant Responses	trees reestablish very slowly (decades or centuries) by seed from sources outside burned area; some sprouting of shrubs and herbs; rapid and prolonged establishment of	prolific resprouting of shrubs and herbs, with very rapid (2 yr) reestablishment of pre-fire cover; little establishment of opportunistic species by seed because of competition from	moderately rapid (5 yr) establishment of shrubs by seed from outside burned area; rapid resprouting of perennial herbs; brief early establishment of a few opportunistic species by seed from

	opportunistic species (including weeds) by seed from outside burned area	established plants and lack of bare soil	outside burned area
Community Structure after 5 Years	no living trees but many standing and fallen snags; moderate cover of resprouting shrubs and herbs; moderate to high cover of opportunistic species including weeds	high cover of resprouting shrubs and perennial herbs; composition and structure similar to pre-fire stands; low cover of opportunistic species	low shrub cover; high cover of resprouting perennial herbs; low to moderate cover of opportunistic species