AN ABSTRACT OF THE THESIS OF

David W. Wrobleski for the degree of Master of Science in Wildlife Science presented on April 15, 1999. Title: Effects of Prescribed Fire on Wyoming Big Sagebrush Communities: Implications for Ecological Restoration of Sage Grouse Habitat.

Abstract approved _____
J. Boone Kauffman

Sage grouse (*Centrocercus urophasianus* Bonaparte) have declined throughout the Great Basin to where listing as a Threatened Species is being considered. Habitat degradation may be a significant cause of this decline. Vegetation structure (shrubs and grasses) influences sage grouse nest success. In addition, the composition, abundance, and phenology of herbaceous dicots and some arthropods influence chick and pre-laying female nutrition. Fire suppression alters these habitat components and the use of prescribed burning may help restore degraded rangelands. Eight- 400 ha plots (4 of which were burned), were sampled before fire in 1997 and in the first year after fire in 1998. In this study the effects of prescribed fire on shrub, grass, and forb composition, cover, and frequency in Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis* Beetle & Young) habitat were examined. In addition, the effects of fire on morphology, abundance, and phenology of 9 dicot species of importance to sage grouse diets were also examined.

Fire burned 47% of treated plots and created ≅ 27 burn/ unburn edges linear km^{-1}. Sagebrush seedling density after fire ranged from 20 to 120 ha^{-1}. Fire increased the reproductive and vegetative vigor of sagebrush along burn edges. Mature sagebrush individuals along burn edges had 361 more reproductive and 177 more vegetative shoots than those away from edges. Cover of perennial grasses was reduced by 4% in burned plots, and only 1% in control plots. Burning did not significantly affect frequency of any grass species. Perennial bunchgrass density was similar between treatments after fire (5.5 vs. 4.8 bunches m^{-2}) . Overall, grasses were likely reduced in size, but not number. Prescribed fire increased percent cover of all forbs ($p=0.012$), but did not significantly change frequency of any individual species. Annual forb cover increased from 3 to 19% in burned plots and 3 to 8% in control plots. Species diversity was not affected by prescribed fire, but burning increased landscape species richness (74 in control plots, 81 in all plots)

Prescribed fire changed the reproductive efforts of herbaceous dicots by resulting in greater mean number of inflorescences and flowers/inflorescence for shaggy milkvetch (*Astragalus malachus* Gray) (9 vs. 6; $p=0.02$, and 23 vs. 21; $p=0.03$ respectively), greater numbers of flowers for microsteris (*Phlox gracilis* Greene) (57 vs. 13; $p=0.01$), greater number of umbels and umbellets for Nevada desert parsley (*Lomatium nevadensis* (Wats.) Coult. & Rose) (4 vs. 2, $p=0.02$; 59 vs. 31, $p<0.01$ respectively), greater numbers of flower heads for Modoc hawksbeard (*Crepis modocensis* Greene) (32 vs. 21; $p=0.07$), and greater flowers cm^{-3} for longleaf phlox (*Phlox longifolia* Nutt.) (0.11 vs. 0.06 cm^{-3}; $p=0.02$).

Burning also resulted in greater crown volume of Modoc hawksbeard (7,085 vs. 4,179cm^3, $p<0.01$) and shaggy milkvetch (2,854 vs. 1,761cm^3, $p=0.09$) and lower crown area of low pussytoes (20 vs. 37cm^2, $p=0.09$).

Frequency (1 vs. 8%), density (0.2 vs. 1 individuals 10^{-2}), and relative abundance (0.4 vs. 2, $p=0.01$) of low pussytoes (*Antennaria dimorpha* Nutt.); and frequency (24 vs. 41%) and relative abundance (12 vs. 24) of longleaf phlox were lower in burned plots ($p=0.01$, $p=0.16$ respectively). Phenology was altered for all the selected species in burned areas; burning extended the period of active photosynthesis later into the growing season ($P<0.01$ for each species). On average, Modoc hawksbeard and Nevada desert parsley flowered 12 – 14 days earlier in burned plots. From 1997 to 1998, average number of ants $trap^{-1}$ increased by 116 in burned plots and only 6 in control plots.

The greater numerical and temporal availability of plant reproductive parts, longer period of photosynthesis, and higher ant abundance would increase sage grouse food availability in burned areas. Due to losses of shrubs in burned areas and reductions in perennial grass cover, nesting cover for sage grouse may be reduced within burned interiors at least the first post-fire year. Elevated numbers of sagebrush shoots and potentially greater herbaceous plant cover along burn edges may offset these losses. Cover for nesting and hiding in unburned areas interspersed with high food availability in burned areas may enhance sage grouse habitat.

Effects of Prescribed Fire on Wyoming Big Sagebrush Communities: Implications for Ecological Restoration of Sage Grouse Habitat

by

David W. Wrobleski

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APPROVED:

Major Professor, representing Wildlife Science

Chair of Department of Fisheries and Wildlife

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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David W. Wrobleski, Author

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CONTRIBUTION OF AUTHORS

Dr. J. Boone Kauffman was involved with the design, analysis, and writing of both manuscripts. Dr. John Crawford was involved in the design of the research for the first manuscript.

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CHAPTER 1

INTRODUCTION

Prescribed fire has become an increasingly integral land management approach in the restoration of degraded rangeland ecosystems. Most of the Intermountain rangelands in the western United States are dominated by big sagebrush (*Artemesia tridentata* Nutt.) (Winward 1980). Wyoming big sagebrush (*A.t. wyomingensis* Beetle & Young) is the most xeric-adapted subspecies of big sagebrush (Winward 1980) and is the dominant species in many ecosystems below 1800m. Historical return intervals of natural fire in Wyoming big sagebrush ecosystems ranged from 32 to 100 years (Wright et al. 1979, Miller et al. 1998).

Sage grouse (*Centrocercus urophasianus* Bonaparte) are native to sagebrush-dominated ecosystems of the western United States (Johnsgard 1983). Sagebrush is their primary food during summer, fall, and winter and provides cover during the entire year (Braun et al. 1977). In addition to sagebrush, sage grouse also use perennial bunchgrasses and forbs (herbaceous dicots) for cover and food, respectively (Wakkinen 1990, Drut et al. 1994b, Gregg et al. 1994, Delong et al. 1995). Residual grass cover around sage grouse nests has been found to be a major factor reducing nest depredation (Gregg et al. 1994, Delong et al. 1995). Herbaceous dicots were used heavily by females before egg laying and may be essential for sage grouse nutrition (Barnett and Crawford 1994). These dicot species, as well as insects, also provide necessary protein for growth of young chicks (Peterson 1970, Johnson and Boyce 1990, Drut et al. 1994a).

Dicot species consumed by sage grouse include mountain dandelion (*Agoseris spp.*), everlasting (*Antennaria spp.*), milkvetch (*Astragalus spp.*), hawksbeard, (*Crepis spp.*), buckwheat (*Eriogonum spp.*), wild lettuce (*Lactuca spp.*), pepperweed (*Lepidium spp.*), desert parsley (*Lomatium spp.*), microsteris (*Phlox gracilis* Greene), phlox (*Phlox spp.*), dandelion (*Taraxacum officinale* Wigg.), and clover (*Trifolium spp.*) in Wyoming big and low sagebrush (*Artemesia arbuscula* Nutt.) habitats (Rogers 1964, Peterson 1970, Barnett and Crawford 1994, Drut et al. 1994a). Leaves and flowers of these and other dicots were found to contain higher amounts of crude protein, calcium, and phosphorus than sagebrush and may be important in sage grouse diets for these reasons (Barnett and Crawford

1994). While the use of grasses and herbaceous dicot species by sage grouse has been demonstrated, little is known of the manner in which fire affects these species.

Since Euro-American settlement, fire suppression and other related anthropogenic factors (e.g. livestock overgrazing) have resulted in increasing density and cover of sagebrush and decreasing grass and forb richness and abundance (Tisdale et al. 1969, Winward 1980, Miller 1989). Land-use activities that reduce grass cover at nests or forb availability for pre-laying female and young sage grouse have been suggested to have a negative impact on sage grouse productivity (Barnett and Crawford 1994, Coggins 1999, Gregg et al. 1994). If habitat management is directed at the persistence of sage grouse in rangelands overpopulated with sagebrush, understory herbaceous vegetation should be increased.

I hypothesized that prescribed fire would enhance forb and grass composition and hence improve sage grouse habitats. However, the pattern of burn on the landscape should result in a mosaic of burned and unburned areas to allow adequate sagebrush to supply cover and food. Thus planning for burned and unburned habitat, and re-establishment of sagebrush on burned areas are essential to maintain long-term sage grouse habitat. In burned areas, prescribed fire can increase native grasses by removing shrub competition, increasing water and nutrient availability, stimulating flowering, and creating suitable areas for seedling establishment (Curtis and Partch 1950, Gill 1981, Sapsis 1990).

Prescribed fire within sagebrush ecosystems may enhance forage potential for sage grouse by increasing the abundance of dicot food species and arthropods, and by altering the morphology and phenology of dicot species. Fire may increase abundance of dicots with adaptations such as seed scarification, or by increasing microsites favorable for germination and establishment (Gill 1981, Kauffman 1990). The increase of nutrients, water, and sunlight following fire has been found to influence plant morphological characteristics such as crown area and crown volume (Daubenmire 1968, Sapsis 1990, Kauffman et al. 1997). Also, in many species, fire increases the reproductive rate of plants by increasing the number of flowers or inflorescences (Curtis and Partch 1950, Stone 1951, Pyke 1983, Kauffman 1990). This could enhance forage quality for sage grouse due to higher nutritional value in reproductive plant parts. Changes following fire include enhanced availability of soil water; increases in available nitrogen, cations, sunlight, reduced competition caused by removal of shrub overstory and herbaceous understory; and a rise in nutrient availability via pyromineralization and ash deposition may also affect plant morphology, and phenology during the first years after fire (Kauffman et al 1997). These changes may cause key forbs to photosynthesize for longer periods during the growing season (Curtis and Partch 1948, 1950, Stone 1951, Daubenmire 1968, Pyke 1983). Sage grouse migration from uplands occurs as vegetation senesces in late summer (Fischer et al. 1996). At these times grouse concentrate in mesic areas such as riparian meadows, lakebed wetlands, or higher elevation sites (Wakkinen 1990). If prescribed fire increases availability of photosynthesizing, succulent foods in uplands during the late summer, available sage grouse habitat may be increased.

At Hart Mountain National Antelope Refuge in southeastern Oregon, the U.S. Fish and Wildlife Service has been working toward the ecological restoration of a diverse rangeland ecosystem.

Livestock grazing was completely eliminated in 1991. This has had positive effects on the understory grasses and forbs in the sagebrush ecosystems (Coggins 1999). To continue the restoration effort in recent years, the USFWS has added active restoration practices in the form of prescribed fire to their passive restoration program. Returning fire to sagebrush ecosystems could restore these areas to the historic balance of ecosystem components which supported an abundance of wildlife species.

The objectives of the study described in the second chapter of were to quantify the first year effects of prescribed fire on species composition, diversity, and shrub, grass and forb abundance between burned and unburned Wyoming big sagebrush stands. The objectives of the work described in the third chapter of were to determine the effects of prescribed fire on the frequency, density, and relative abundance (overall abundance) of selected forb species used by sage grouse. Also, to describe their morphology (size and number of flowers), phenology (length of time available and length of time flowering). I also examined the abundance of ground-dwelling arthropods important in the diet of sage grouse.

CHAPTER 2

EFFECTS OF PRESCRIBED FIRE IN WYOMING BIG SAGEBRUSH COMMUNITIES: IMPLICATIONS FOR ECOLOGICAL RESTORATION OF SAGE GROUSE HABITAT

Abstract

Sage grouse (*Centrocercus urophasianus* Bonaparte), once abundant in the western United States, are now being considered for listing as a threatened species. We examined the effects of ecological restoration in the form of prescribed fire on the composition, cover, and diversity of shrubs, grasses, forbs of sage grouse habitat in Wyoming big sagebrush (*Artemesia tridentata wyomingensis*) habitat at Hart Mountain National Antelope Refuge, OR. Eight similar plots, ≅ 400 ha in size, were sampled before fire in 1997 and after fire in 1998. Four randomly selected plots were burned in September, 1997. Fire burned 47% of treated plots and created ≅27 burn/ unburn edges linear km^{-1}. Density of sagebrush seedlings after fire ranged from 20 to 120 ha^{-1}. Fire increased the reproductive and vegetative vigor of sagebrush along burn edges. Mature sagebrush individuals along burn edges had 361 more reproductive and 177 more vegetative shoots than those away from edges. Fire reduced cover of perennial grasses by 4%, in burned plots while only a 1% decrease was observed in control plots, but this is likely a short-term effect. Burning did not significantly affect frequency of any grass species. Perennial bunchgrass density was similar between burned and control plots (5.5 vs. 4.8 individuals m^{-2}) in the first post-fire year. Cover of annual forbs increased from 3 to 19% in burned plots and from 3 to 8% in control plots, but burning did not significantly affect frequency of any forb species. Fire caused no changes in alpha diversity (species $transect^{-1}$) or gamma diversity (species $plot^{-1}$), however the combination of burned and unburned areas on the landscape increased species richness. Increased forb cover, potential increases in cover on burn edges due to greater numbers of shoots, and a mosaic of burned and unburned habitats may have positive effects on habitat for sage grouse.

Introduction

Sage grouse (*Centrocercus urophasianus*) are native to sagebrush-dominated (*Artemesia* spp.) ecosystems of the western United States (Johnsgard 1983). Sagebrush is their primary food during

summer, fall and winter, and provides cover during the entire year (Braun et al. 1977). Sage grouse also use bunchgrasses and forbs (non-graminoid, herbaceous species) for cover and food, respectively (Drut et al. 1994b, Gregg et al. 1994, Delong et al. 1995). Because of their higher protein and nutrient content, forbs are considered essential for the nutrition of females before egg laying (Barnett and Crawford 1994). Both forbs and insects provide necessary protein for growth of young chicks (Peterson 1970, Johnson and Boyce 1990, Drut et al. 1994a).

Historical return intervals of fire in Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems range from 32 to 100 years (Wright et al. 1979, Miller et al. 1998). In many areas, such as southeastern Oregon, fire frequency has been drastically reduced by fire suppression and related anthropogenic factors, such as livestock overgrazing. This has resulted in increases in the density and cover of sagebrush with a concomitant decrease in understory grass and forb species (Tisdale et al. 1969, Miller 1989). Sage grouse nest success has been related to the height of residual grass cover around nests (Gregg et al. 1994, Delong et al. 1995). Reductions of residual grass cover at nests, and fewer forbs for pre-nesting females and young chicks, have been associated with low productivity of sage grouse populations (Barnett and Crawford 1994, Gregg et al. 1994). If ecological restoration is directed at the persistence of sage grouse in degraded rangelands enhancement of understory herbaceous vegetation is necessary.

At Hart Mountain National Antelope Refuge in southeastern Oregon, the U.S. Fish and Wildlife Service has been working toward the ecological restoration of this rangeland ecosystem. Livestock grazing was removed from the refuge in 1991. This has had positive effects on the understory grasses and forbs in the sagebrush ecosystems (Coggins 1999). To further this restoration effort in recent years, the USFWS has added active restoration practices such as reintroducing prescribed fire. Reintroducing fire to sagebrush ecosystems could restore these areas to the historic balance of ecosystem components which supported an abundance of wildlife species.

I hypothesized that prescribed fire can enhance forb and grass composition in a Wyoming big sagebrush ecosystem. In burned areas, prescribed fire can increase native grasses by removing shrub competition, increasing water and nutrient availability, stimulating flowering, and increasing abundance (Curtis and Partch 1950, Gill 1981, Sapsis 1990). Many dicot species establish after fire because of adaptations such as seed scarification, or bare mineral soil requirements for germination (Gill 1981, Kauffman 1990).

Our objectives were to quantify the first-year effects of prescribed fire on species composition and canopy cover of shrubs and percent cover and composition of grasses and forbs between burned and unburned Wyoming big sagebrush stands at the Hart Mountain National Antelope Refuge, Oregon.

Study Area

Plant response to prescribed fire was evaluated on 4 burned and 4 control plots in a Wyoming big sagebrush ecosystem. Four plots were chosen randomly for prescribed fire treatment. Plots were ≅400ha in size and located in the northeastern portion of Hart Mountain National Antelope Refuge, OR (Figure 1). Elevation of the study plots ranged from 1,550 m to 1,615 m with level topography. Soils were a cobbly clay-loam of the Ratto-Coglin complex, Ratto series (SCS 1991). Mean temperature between March and July on the study area was 13°C. Mean annual precipitation at refuge headquarters was 29 cm (Drut et al. 1994a). Precipitation was 24.9 and 45.6 cm in 1997 and 1998 respectively (U.S.F.W.S. Unpubl. Data). Study plots have not been grazed by livestock since 1991, and not burned for >50yrs (U.S.F.W.S. Unpubl. data). Dominant grasses in the study plots were bottlebrush squirreltail (*Elymus elymoides* Rafin.), and Sandberg's bluegrass (*Poa sandbergii* Vasey). Small communities dominated by low sage (*Artemesia arbuscula* Nutt.), basin big sagebrush (*A.t.* ssp. *tridentata*), or grasses were found within the study areas but were not sampled.

Methods

Prescribed Fire Treatment

Before, during, and after ignition of prescribed fires, information about weather, fuels, and fire behavior were collected. Weather data (temperature, relative humidity, wind speed, cloud cover, and precipitation) were collected on the burn plots during prescribed burning with a belt weather kit. Pre-fire understory biomass was measured by clipping 25– 20x50cm randomly-located micro-plots in each plot, drying at 50°C and weighing the material. This was repeated after the fires to obtain post-fire understory biomass. Understory fuel consumption was calculated as the percentage of biomass lost due to fires. Pre-fire biomass of Wyoming big sagebrush in each burn plot was determined with the following equation:

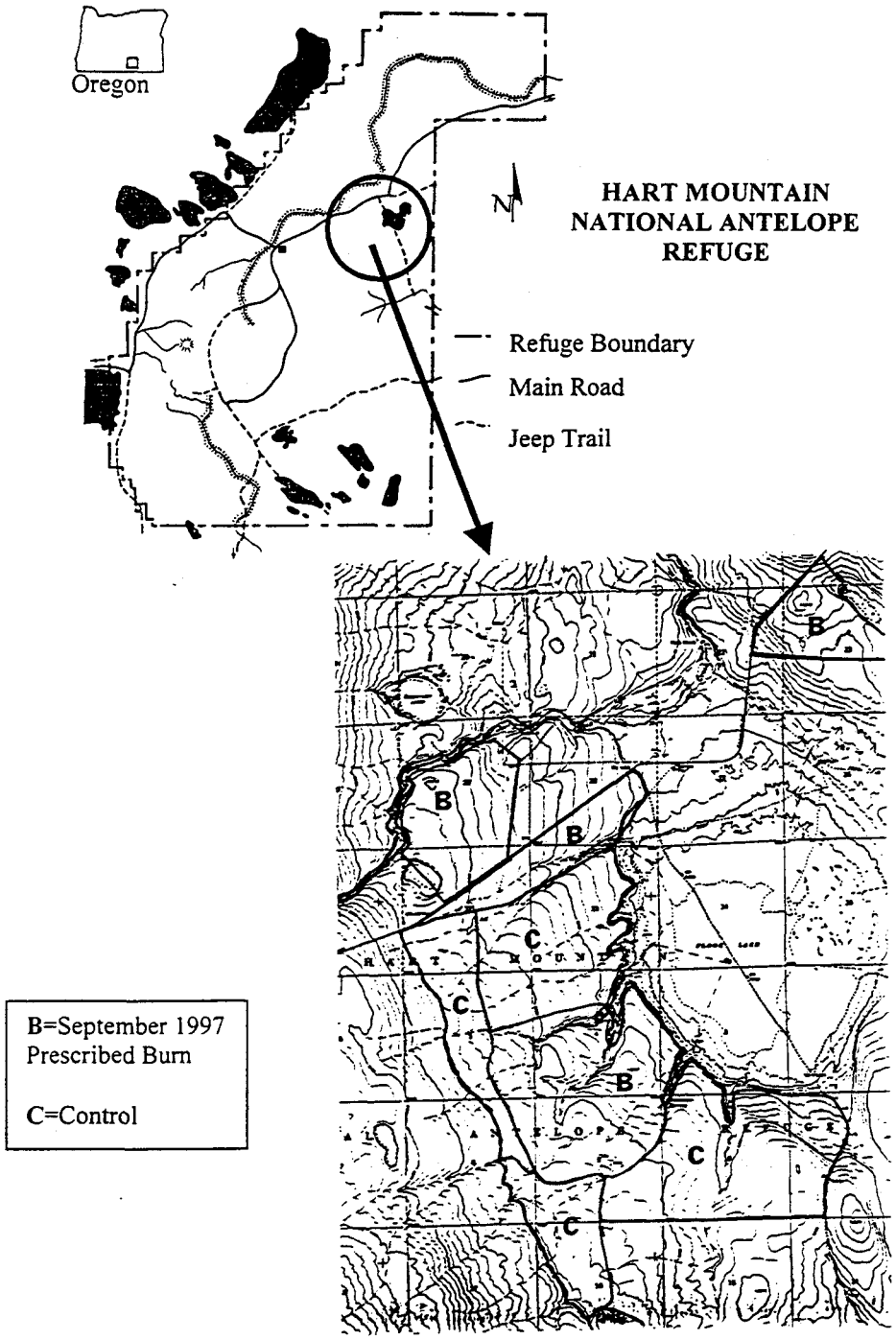

Figure 1. Hart Mountain National Antelope Refuge in southeastern Oregon with September 1997 prescribed burn and control experimental plots.

$$\text{Total Fuel Biomass (kg ha}^{-1}) = -2419.043 + 93.548\,(L) + 62.537\,(H)$$

Where (L) = the line intercept canopy cover of Wyoming big sagebrush and (H) = the height of sagebrush in cm (Champlin 1983). Fuel moisture of understory as a proportion of dry weight was measured by clipping and drying 10 random, 20x50 cm samples of understory in each plot immediately before ignition of fires. Ten-hour moisture sticks were used to estimate moisture of dead 10-hour fuels (n=3). Flame height, flame length, flame depth, rate of spread, and residence time were measured by observation during each fire (Alexander 1982). Line intercept was used to measure percent area burned along 5 transects beginning at a random starting point and crossing the plot in a random direction on 1"/1000' infrared aerial photos (Brower et al. 1990). Because sage grouse require sagebrush interspersed with open patches on the landscape (Braun et al. 1977), the number of burned/ unburned edges linear km^{-1} in treatment plots were quantified along 15 similar transects.

Community Composition

All plots were sampled before fire in 1997 and in the first post-fire year, 1998. Percent cover and frequency of species were measured along 48-50 randomly placed 20-m transects in each study plot and year. In 1998, location of random transects was restricted to burned areas within treatment plots. Percent cover of shrubs was measured with the line intercept technique (Canfield 1941). All shrubs intercepting the transect were also measured from the ground and classified into 1 of 3 height classes: short (<40 cm), medium (40 - 80 cm), tall (>80 cm) because of the importance of medium height shrubs for sage grouse nesting habitat (Gregg et al. 1994). In burned plots before prescribed fires, density of shrubs was estimated with the point quarter method (n=25/plot) (Brower et al. 1990). Seedling density of sagebrush after prescribed fire was measured by counting the individuals in 10- 100x100cm plots located along each transect.

The frequency and cover of grasses and forbs were measured with 10-20x50-cm microplots placed at regular intervals along each 20-m transect (Daubenmire 1959). Cover of litter and bare ground were also measured in these micro-plots. Grasses with droop height (excluding flower stalks) ≥18 cm (tall) and those < 18cm (short) were distinguished, because this height was found to be the minimum cover needed to reduce to the chance of sage grouse nest depredation (Wakkinen 1990, Gregg et al. 1994). To further quantify initial effects of fire, perennial bunchgrass density was measured in 10 - 20m x 1m strip-plots in each study plot after fire during 1998 by counting the number of individuals of short (*Poa secunda* Vasey) and tall (all others) species.

I measured species diversity at 3 spatial scales; alpha diversity (# species/transect), gamma diversity (# species/plot), and heterogeneity (or beta diversity, gamma/alpha) in each burn treatment and control plot (Whittaker 1967). Plant species detected within the study areas were assigned to one or more fire guilds based on their adaptive strategies to survive fire events (Havlina 1995). Fire guilds were described as the ecological traits facilitating survival of the species or individual after fire. The fire guilds assigned were evaders (on site seed storage), endurers (resprout from crowns or roots), avoiders (recover very slowly fire), invaders (high rates of seed dispersal into burned areas), and resisters (protected from fire by bark or other tissues) (Agee 1993).

Response of Sagebrush Along Ecotones to Fire

Big sagebrush does not sprout, and is easily killed by fire (Blaisdell 1953). I quantified response of Wyoming big sagebrush along burn edges to prescribed fire. Twenty-five sagebrush plants along burn edges were paired with 25 unaffected interior plants and sampled in each of the 4 treatment plots. Edge (treated) sagebrush individuals were immediately adjacent to the burned areas, yet had <25% of their canopy killed by the fire. Interior plants (untreated) were located at least 10-m from all burn edges but within 20-m of the paired treated plant. The number of vegetative and reproductive shoots were counted within a 20x20-cm frame centered over the stem base of sagebrush plants (Miller et al. 1991). Data were converted to number of shoots m^{-2} of canopy (Miller et al. 1991). Mean differences between numbers of reproductive, vegetative, and total shoots were compared between edge and interior plants with Wilcoxon signed-rank tests due to the low number of pairs (N=4 plots). Number of reproductive and number of vegetative shoots of sagebrush were log-transformed because the plants at the burn edge had larger variances corresponding with larger means (Ramsey and Schafer 1997:65). Confidence intervals (α=0.10) were also calculated on mean differences in shoot abundance between edge and interior plants in each treatment plot.

Analysis of Herbaceous Composition

To describe if certain groups of species were important in delineating treatment effects, an ordination was performed on percent cover of all species in the 8 plots during the pre- and post-treatment years. Skewness, kurtosis, and coefficients of variation were examined in PCord (McCune

and Mefford 1997). Because of high variation (CV >300%), species found in fewer than 3 of the 16 plot/year combinations were excluded from ordination (McCune 1998). Data were then relativized by the maximum percent cover in each species (McCune 1998), and principal components analysis was performed using the variance/ covariance matrix.

Next I tested plant cover response to fire by each life form (forb, grass) separately with multivariate analysis of variance (MANOVA) (Tabachnick and Fidell 1996). Three dependent variables (DVs) were created within the grasses: perennial, tall (>18cm), and annual. Forb cover was also divided into 3 DVs: primary sage grouse foods (*Agoseris* spp., *Antennaria* spp., *Astragalus* spp., *Crepis* spp., *Eriogonum* spp., *Lomatium* spp., *Microseris* spp., *Phlox gracilis* Greene, *P. longifolia* Nutt., *Tragopogon* spp., and *Trifolium* spp.), perennial, and annual forbs. Grass density data were separated into taller species and Sandberg's bluegrass and compared between burn and control with MANOVA.

In comparing the above dependent variables between treatment and control for pre- and post-fire years with MANOVA, the YEAR term indicated differences between years, the PLOT term indicated pre-existing differences between treatment and control plots, and the YEAR X PLOT interaction indicated an effect caused by prescribed fire (i.e. differing year effects by treatments). Analysis of variance (ANOVA) was then used to assess the effect of prescribed fire on each individual dependent variable. Diversity of the study plots was analyzed with MANOVA. Gamma and alpha diversity were used as dependent variables, and then tested individually with ANOVA. To determine if prescribed fire affected individual herbaceous species, percent frequency was compared between treatments and years with factorial ANOVA (year, plot, year*plot) for each species with >5% frequency in both treatments before fires. All tests were considered significant at α=0.10 to reduce type II error rate.

Results

Prescribed Fire Treatment

The prescribed fire plots were ignited with a heli-torch September 23-28, 1997 utilizing strip-head or ring-fire ignition patterns (Martin 1990). Ambient temperature during fires ranged from 19° to 28°C, relative humidity ranged from 17 to 24%, wind speed ranged from 6.4 to 9.7km h^{-1}, cloud cover was <10%, and there had been no precipitation for > 2 weeks. Pre-fire understory biomass in the burned plots ranged from 1,260-1,820 kg ha^{-1} and overstory biomass was 3,444± 106 kg ha^{-1}.

In the post-fire mosaic there were 27± 2.0 edges linear km^{-1}. Thus, along a transect, a burn/unburn edge was crossed every 37m. Approximately 47% (range=36-62%) of the area within the treated plots was burned. Within burned areas all sagebrush biomass was consumed. Thus throughout the treatment plots 1619± 50 kg ha^{-1} of sagebrush remained after fire. Understory consumption was 80± 8% within burned portions of treatment plots, and 37± 4% throughout the entire area of the burned plots. Understory fuel moistures for the dead herbaceous vegetation ranged from 4.4-6.5%; moisture of 10-hour dead fuels ranged from 5.5-8.0%. Flame height ranged from 2-3.7m, flame length ranged from 2-4.4m, flame depth ranged from 2-7.8m, rate of spread ranged from 4.6-12 m/min, and residence time ranged from 0.6-2.6 minutes. Mean estimate of Byram's fireline intensity was 1,321 kW m^{-1}, reaction intensity was 302 kW/m^2 (Alexander 1982).

Shrub Response to Fire

Total shrub cover before treatment was 26± 1.6% in treatment plots and 24± 1.5% in control plots. After one year shrub cover in control plots increased significantly to 27± 0.6% (t-test, p=0.054). Sagebrush cover (22%) on all plots before treatment comprised 87% of total shrub cover. Other common shrubs on the study plots before treatment (2.7% total cover) were spiny hopsage (*Atriplex spinosa* Collotzi), and broom snakeweed (*Guiterriza sarothae* Britt. & Rusby).

Pre-fire shrub density in burned plots ranged from 16,063 to 29,091 individuals ha^{-1}. Fire killed all sagebrush plants within burned portions of treated plots (47± 12% of the area). However, in burned areas, a range of 20 to 120 sagebrush seedlings ha^{-1} were present the first post-fire year. Although none were sampled in the transects, scattered spiny hopsage individuals were observed to be germinating, and cottonhorn horsebrush (*Tetradymia spinescens* H. & A.) seedlings were also observed.

Number of reproductive shoots (257 vs. 80), vegetative shoots (510 vs. 149), and total shoots (767 vs. 229) per plant were significantly greater among plants along burn edges than among plants in unburned interior (Wilcoxon sign rank p=0.0078) (Figure 2). Thus prescribed fire elevated the number of total shoots of sagebrush individuals along burn edges by 243± 29% more than sagebrush individuals in unburned interior.

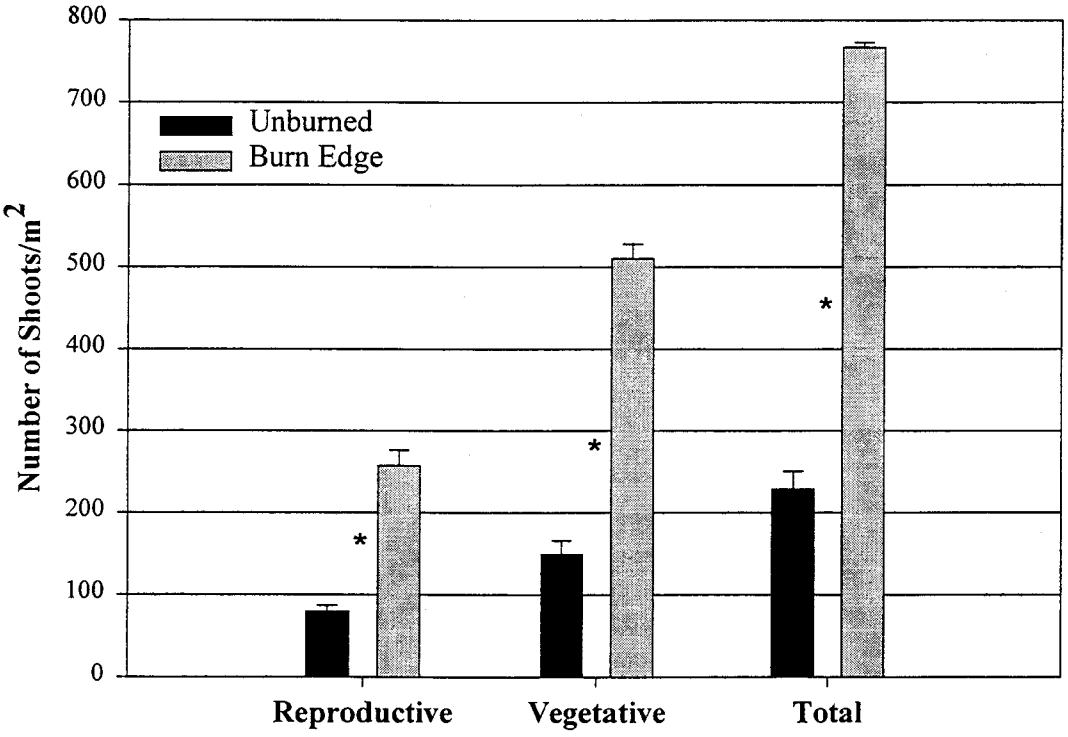

Figure 2. Mean numbers of reproductive, vegetative, and total shoots of Wyoming big sagebrush plants (+SE) along the immediate edge of a September, 1997 prescribed fire compared to sagebrush plants in the unburn interior (>10m away from edge). An * indicates significance at α=0.10

Grasses

Prescribed fire decreased overall cover of grasses (MANOVA, p=0.13). Cover of perennial grasses declined by 4% (9% in 1997 to 5% in 1998) in burned plots, while there was only a 1% change (10% in 1997 to 9% in 1998) in control plots (p=0.027) (Figure 3). Burning had no significant effect on cover of tall grasses (<2% decrease in burn vs. no change in control plots) or annual grasses (1-2% in all treatments and years). Density of tall perennial bunchgrasses (2.7 m^{-2} in burn, 2.2 in control) and Sandberg's bluegrass (2.8 m^{-2} in burn, 2.6 in control) in the post-treatment year (1998) was not significantly different between prescribed burn and unburned control plots (Figure 4).

Of 8 grass species observed, Sandberg's bluegrass (45% pre-fire frequency), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) (45% pre-fire frequency), and cheatgrass (18% pre-fire frequency) were not significant different between burn and control plots (Table 1).

Forbs

Prescribed fire caused significant increases in the percent cover of forbs (forbs selected by sage grouse, perennial, and annual forbs) (MANOVA, p=0.012). Prescribed fire increased cover of annual forbs by 16% (3% in 1997 to 19% in 1998) in burned plots, while only a 5% increase (3% in 1997 to 8% in 1998) was observed in the control plots (p=0.003) (Figure 5). No significant differences were detected in cover of grouse foods or perennial forbs.

Of the 20 annual forb species observed on the study area, only microsteris (13% pre-fire frequency), and blue-eyed mary (*Collinsia parviflora* Lindl.) (37% pre-fire frequency) were found frequently enough before fires to be tested for significance (Table 1). Forty species of perennial forbs were observed. Modoc hawksbeard (*Crepis modocensis* Greene), longleaf phlox (*Phlox longifolia* Nutt.), wild onion (*Allium spp.*), milkvetch (*Astragalus spp.*), dwarf yellow fleabane (*Erigeron chrysopsidis* Gray), and desert parsley (*Lomatium spp.*) were tested for significance. Fire caused no significant changes in the frequency of any annual or perennial forb species (Table 1, Figure 6).

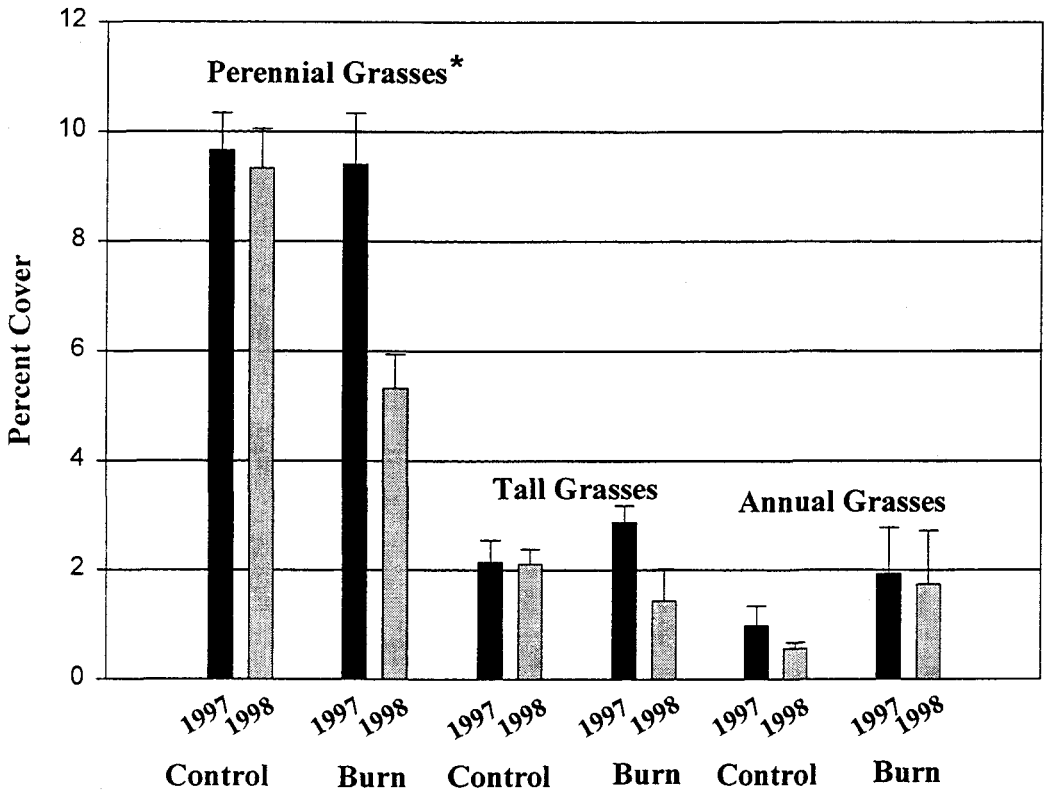

Figure 3. Mean (+SE) cover of annual, perennial, and tall grasses in burn and control plots during pre-treatment sampling (1997) and post-treatment sampling (1998) in a Wyoming big sagebrush ecosystem. An * indicates significance at α=0.10.

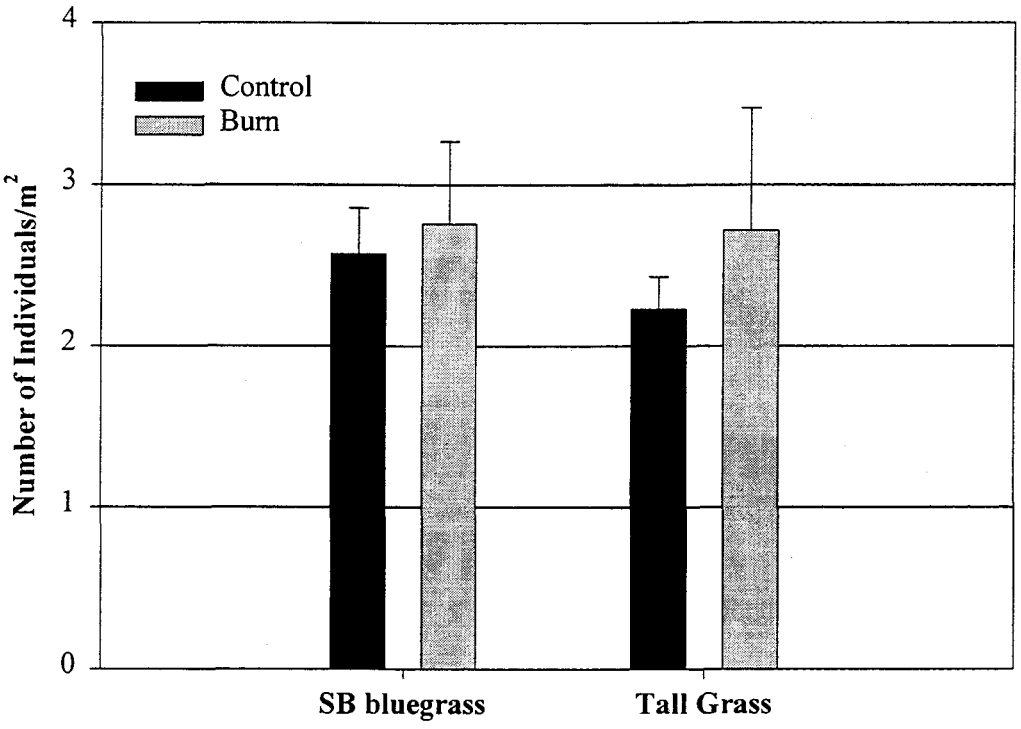

Figure 4. Number of Sandberg's bluegrass, and tall grasses (other perennial bunchgrasses) individuals m^{-2} (+SE) in prescribed fire treatment and control plots during 1998 in a Wyoming big sagebrush ecosystem.

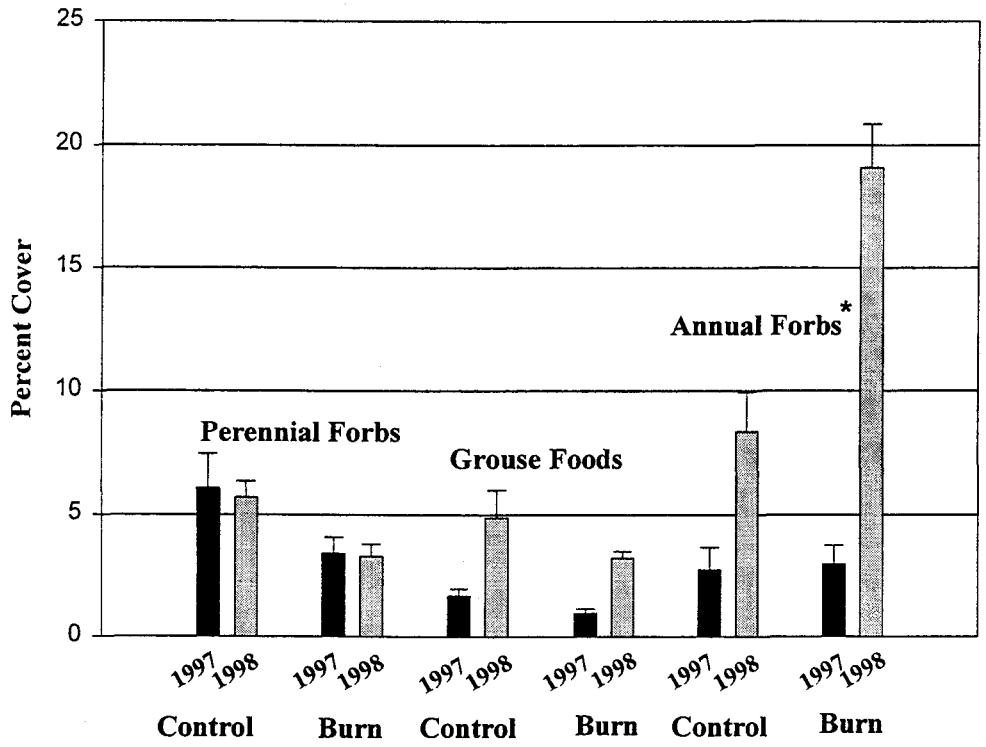

Figure 5. Mean (+SE) cover of sage grouse foods, perennial, and annual forbs in burn and control plots during pre-treatment sampling (1997) and post-treatment sampling (1998) in a Wyoming big sagebrush ecosystem. An * indicates a significant difference at α=0.10.

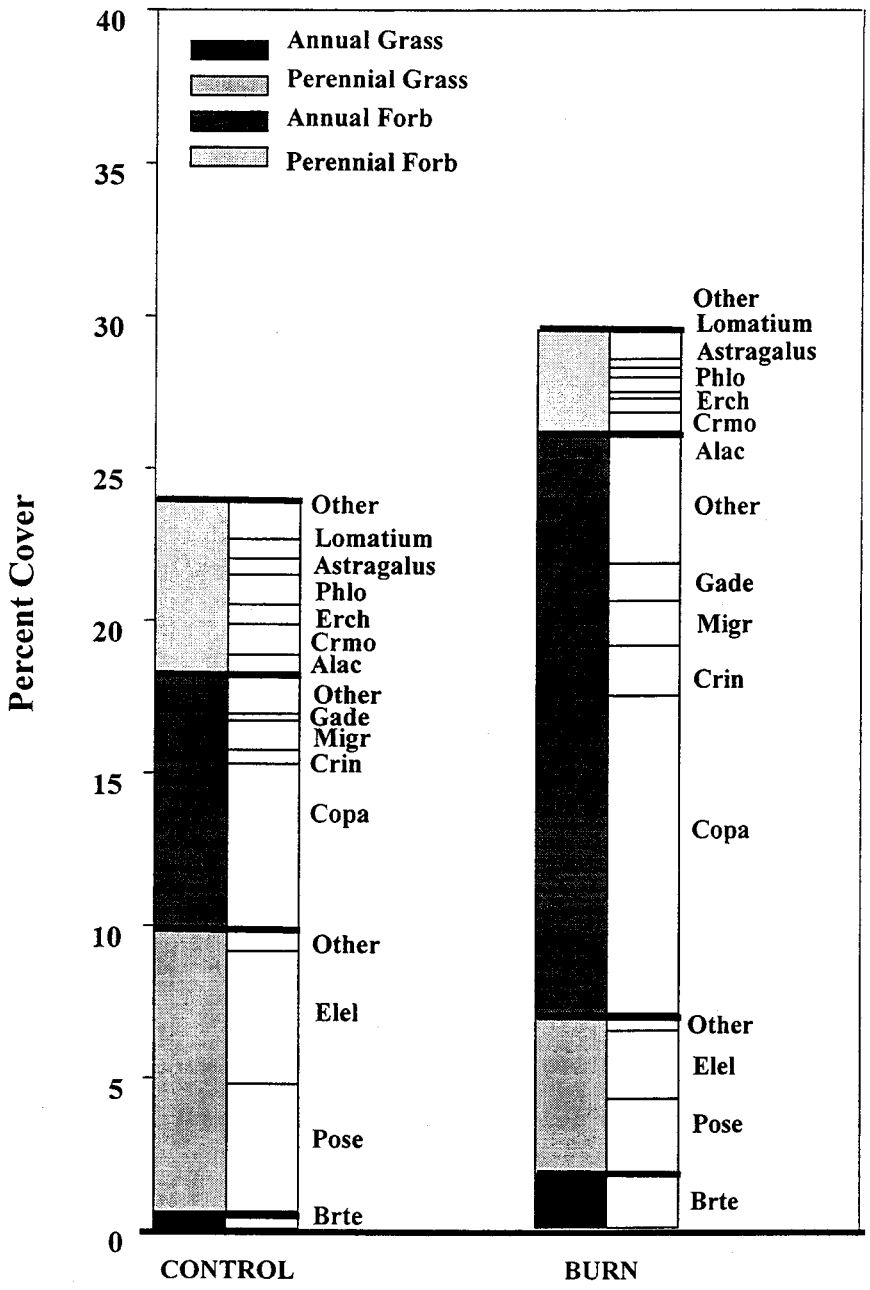

Figure 6. Percent cover of growth-form groups and abundant plant species in the control and burn plots within the Wyoming big sagebrush study area during 1998.

Table 1. Percent frequency (±SE) of herbaceous species observed in control and burn plots during 1997 and 1998 in a Wyoming big sagebrush community.

Species Name	Species Code	Control 1997	±SE	Control 1998	±SE	Pre-Burn 1997	±SE	Post-Burn 1998	±SE
Grasses									
Achnatherium hymenoides	Achy	0.3	0.2	0.2	0.1	0.7	0.2	0.6	0.2
Achnatherium thurberianum	Acth	2.4	1.1	1.4	0.6	2.6	0.5	2.4	0.3
Bromus tectorum†	Brte	16.5	4.5	15	2.8	20.6	6.3	19.1	7.0
Elymus elymoides†	Elel	48.0	0.8	42.9	1.0	44.2	1.4	24.7	3.5
Elymus lanceolatus+ *Pseudoroegneria spicata***		4.8	2.2	5.4	1.6	5.1	2.3	2.5	0.9
Elymus lanceolatus	Ella	-	-	4.9	1.5	-	-	2.0	0.9
Festuca idahoensis	Feid	3.9	0.6	2.1	0.5	3.2	1.0	1.9	1.0
Poa secunda†	Pose	55.3	4.2	44.3	3.3	39.8	7.4	33.0	7.1
Pseudoroegneria spicata	Pssp	-	-	0.5	0.2	-	-	0.5	0.3
Species Richness				8				8	
Perennial Forbs									
Agoseris glauca	Aggl	11.0	4.0	0.5	0.3	4.7	1.6	0.2	0.1
*Allium spp.***†		13.4	1.3	22.6	3.0	10.8	1.2	18.8	3.9
A. acuminatum	Alac	-	-	20.8	3.1	-	-	16.9	4.0
A. lemmonnii	Alle	-	-	1.8	0.9	-	-	1.9	0.4
Antennaria dimorpha	Andi	1.8	0.5	2.2	0.6	1.2	0.3	0.4	0.1
Arabis holboellii	Arho	0.8	0.3	1.2	0.1	1.6	0.2	0.3	0.1
Arenaria aculeata	Arac	0.5	0.4	0.5	0.2	0	-	0	-
Aster scopulorum	Assc	1.1	0.9	0	-	0.2	0.2	0	-
Astragalus spp. †		10.7	1.0	9.6	1.7	5.8	1.7	6.5	0.9
A. malachus	Asma	-	-	3.3	1.0	-	-	3.6	1.2
A. obscurus	Asob	-	-	3.1	0.9	-	-	0.5	0.2
A. purshii	Aspu	-	-	3.2	1.1	-	-	2.4	0.5
Balsamorhiza saggitata	Basa	0.1	0.1	0.3	0.2	0.1	0.1	0.2	0.1
Castilleja rustica	Caru	1.2	0.5	0.7	0.2	0.7	0.1	0.3	0.3
Chaenactis douglasii	Chdo	1.2	1.0	0.1	0.1	0.1	0.1	0.1	0.1
Crepis spp.		16.8	3.0	23.5	6.1	5.5	0.8	9.3	1.8
C. acuminata	Crac	-	-	1.2	0.1	-	-	0.4	0.3
C. modocensis†	Crmo	-	-	22.3	6.1	-	-	8.9	1.9

Table 1. Continued

Species Name		Control 1997	±SE	Control 1998	±SE	Pre-Burn 1997	±SE	Post-Burn 1998	±SE
Delphinium nuttalianum	Denu	2.4	1.1	3.7	1.2	2.9	1.6	8.6	5.1
Erigeron spp.		15.4	2.1	13.6	2.8	7.0	2.1	4.2	0.8
Erigeron chrysopsidis†	Erch	-	-	12	2.8	-	-	4	0.8
E. lanatus	Erla	-	-	0.1	0.1	-	-	0	-
E. linearis	Erli	-	-	1.5	0.2	-	-	0.2	0.1
Eriogonum spp.		9.6	1.9	8.6	0.8	4.4	1.4	0.6	0.7
E. cespitosum	Erce	-	-	0.2	0.1	-	-	0	-
E. ovalifolium	Erov	-	-	8.4	0.4	-	-	0.6	0.2
Lewisia rediviva	Lere	0.4	0.2	1.1	0.6	0.2	0.1	1.1	0.6
Lomatium spp.†		9.3	3.3	14.8	2.6	7.4	1.6	6.2	2.5
L. canbyii	Loca	-	-	2.6	2.1	-	-	0.3	0.2
L. donnelli	Lodo	-	-	3.7	1.9	-	-	0.4	0.4
L. nevadense	Lone	-	-	4.9	3.0	-	-	4.9	2.7
L. vaginatum	Lova	-	-	0	-	-	-	0.1	0.1
L. watsonii	Lowa	-	-	3.6	2.5	-	-	0.5	0.2
Oenethera boothii	Oebo	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2
Microseris troximoides	Mitr	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1
Orobanche fasciculata	Orfa	0.1	0.1	0	-	0	-	0	-
Penstemon spp.	Pens	0	-	0	-	0.1	0.1	0.1	0.1
Phlox spp.		24.6	5.4	24.5	4.1	16.1	3.7	10.9	1.9
P. longifolia	Phlo	-	-	24.1	3.9	-	-	10.7	2.0
P. muscoides	Phmu	-	-	0.4	0.4	-	-	0.2	0.2
Phoenicaulis cherianthoides	Phch	0.1	0.1	0	-	0.3	0.3	0	-
Ranunculus spp.		0.8	0.4	1.2	0.8	1.2	0.6	0.8	0.3
R. glaberrimus	Ragl	-	-	0.4	0.2	-	-	0	-
Senecio integerrimus	Sein	0	-	0	-	0.1	0.1	0	-
Stenotus stenophyllus	Stst	0.4	0.4	0.1	0.1	0	-	0	-
Tragopogon dubious	Trdu	0	-	0	-	0	-	0	-
Trifolium macrocephalum	Trma	0.6	0.6	0	-	0	-	0	-
Unknown Forb		1.9	0.8	2	.4	2.3	0.5	2.3	0.7
Unknown grass		0.3	0.3	0	-	0	-	0	-
Zygadenus venenosus	Zyve	0.2	0.1	0.1	0.1	0.1	0.1	0	-
Species Richness				32				27	

Table1. Continued

Species Name	Species Code	Control 1997	±SE	Control 1998	±SE	Pre-Burn 1997	±SE	Post-Burn 1998	±SE
Annual Forbs									
Amsinckia menziesii	Amme	0	-	0.2	0.2	0	-	0.1	0.1
Blepharipappus scaber	Blsc	2.1	1.8	1.0	0.9	0	-	0.4	0.4
Camelina microcarpa	Cami	0	-	0	-	0	-	0.1	0.1
Chenopodium spp.	Chen	0	-	0	-	0	-	0.4	0.4
Collinsia parviflora†	Copa	24.3	8.4	68.3	10.8	30.3	5.2	71.1	11.0
Cryptantha circumcissa	Crci	0	0	0.2	0.2	0	0	0.25	0.1
C. intermedia	Crin	3.7	0.6	14.2	2.1	6.8	1.4	21.3	4.6
Descaurania richardsonii	Deri	2.5	0.5	17.3	2.3	3.1	0.8	32.1	1.2
Draba verna	Drve	0	-	0.1	0.1	0	0	0.3	0.2
Epilobium minutum	Epmi	5.3	1.8	7.8	2.4	2.8	1.5	4.3	0.3
Eriastrum sparsiflorum	Ersp	0.9	0.4	3.3	1.2	1.6	0.9	4.3	1.2
Eriogonum vineminum	Ervi	-	-	1.3	0.9	-	-	1.1	0.6
Erucastrum gallicum	Erga	-	-	0	-	-	-	0.2	0.1
Gayophytum decipiens	Gade	0.5	0.4	4.5	1.9	0.5	0.3	9.8	1.4
Gilia sinuata	Gisi	0.2	0.2	3.0	1.2	0.4	0.3	13.5	3.6
Lappula spp.	Lapp	0	-	0	-	0.1	0.1	0	-
Layia glandulosa	Lagl	0	-	0	-	0.1	0.1	0	-
Lepidium perfolatum	Lepe	0.5	0.2	0.6	0.4	1.8	1.3	0.2	0.1
Lithophragma bulbifera	Libu	0.1	0.1	0	-	0	-	0	-
Lupinus pusillus	Lupu	3.1	1.0	6.2	1.1	3.3	1.0	6.3	1.0
Mentzelia albicaulis	Meal	-	-	1.6	0.4	-	-	3.2	1.2
Mimetanthe pilosa	Mipi	0.3	0.2	0.9	0.7	0	0	2	0.9
Mimulus nanus	Minu	0	-	0.3	0.2	0	-	0.3	0.1
Navarretia intertexta	Nain	0	-	0.1	0.1	0.1	0.1	0.1	0.1
Phacelia linearis	Phli	1.3	0.6	2.5	1.2	0.4	0.3	5.1	1.8
P. lutea	Phlu	-	-	0.3	0.2	-	-	0.8	0.4
Phlox gracilis†	Phgr	9.2	3.8	17.5	5.7	11.6	4.0	23.0	4.1
Plectectris macrocepha	Plma	1.1	0.9	1.5	1.0	0.7	0.6	0.9	0.4
Polemonium micranthum	Pomi	-	-	0.5	0.4	-	-	0.6	0.2
Ranunculus testiculatus	Rate	-	-	0.8	0.6	-	-	0.8	0.3
Scutellaria nana	Scna	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1
Species Richness				25				28	

* Taxonomy of *Agropyron* split into separate genera.

** Some vegetation only identified to genus-level in 1997.

† Tested for significance, no fire effects detected

Species Composition

The relative abundance of annual and perennial plants was a major force driving the separation of the 8 experimental plots in multivariate space. Principal components analysis explained 32.2% and 15.6%, (cumulative total 47.8%) of the variance in the percent cover data along the first 2 axes. The primary axis along which the plots are distributed represents a gradient from high cover of perennial to annual plants (Table 2, Figure 7). In 1998 the control plots were located in the direction of greater cover of annual plants such as blue-eyed mary, mountain tansy-mustard (*Descaurania richarsonii* (Sweet) Schulz.), microsteris, white-stemmed mentzelia (*Mentzelia albicaulis* Dougl.), and sinuate gilia (*Gilia sinuata* Dougl.); but with the addition of fire, the burned plots moved much further along this axis.

The second axis represents a gradient towards increased abundance of species such as prickly sandwort (*Arenaria aculeata* Wats.), dwarf yellow fleabane, sagebrush buttercup (*Ranunculus glaberrimus* hook.), and species of *Lomatium* (e.g. *Lomatium donnellii* Coult. & Rose) which were more common in the Floke-Ratto soils adjacent to the study plots. The distribution of the plots along the second axis closely corresponds with their distance from the Floke-Ratto soil boundary, which explains the higher abundance of species common in that soil type.

Table 2. Most influential species loadings of percent cover data in the Wyoming big sagebrush community from principal components analysis. Species and eigenvectors listed for the first axis are those which most clearly separated the treatment/year groups along the gradient from annual to perennial species. Species listed for the second axis were those which became increasingly prevalent near the Floke-Ratto/ Ratto-Coglin soil type boundary.

Percent Cover			
Axis 1		**Axis 2**	
Species	**Eigenvector**	**Species**	**Eigenvector**
Gayophytum decipiens	0.27	*Lomatium spp.*	0.31
Descaurainia richardsonii	0.25	*Arenaria aculeata*	0.30
Collinsia parviflora	0.23	*Epilobiun minutum*	0.26
Mimulus nanus	0.21	*Erigeron chrysopsidis*	0.23
Mentzelia albicaulis	0.16	*Plectritis macrocepha*	0.22
Eriastrum sparsiflorum	0.20	*Phacelia linearis*	-0.07
Bare ground	0.20	*Atriplex spinosa*	-0.11
Microsteris gracilis	0.19	*Castilleja rustica*	-0.21
Lupinus pusillus	0.17		
Gilia sinuata	0.15		
Litter	-0.22		
A.t. wyomingensis	-0.28		

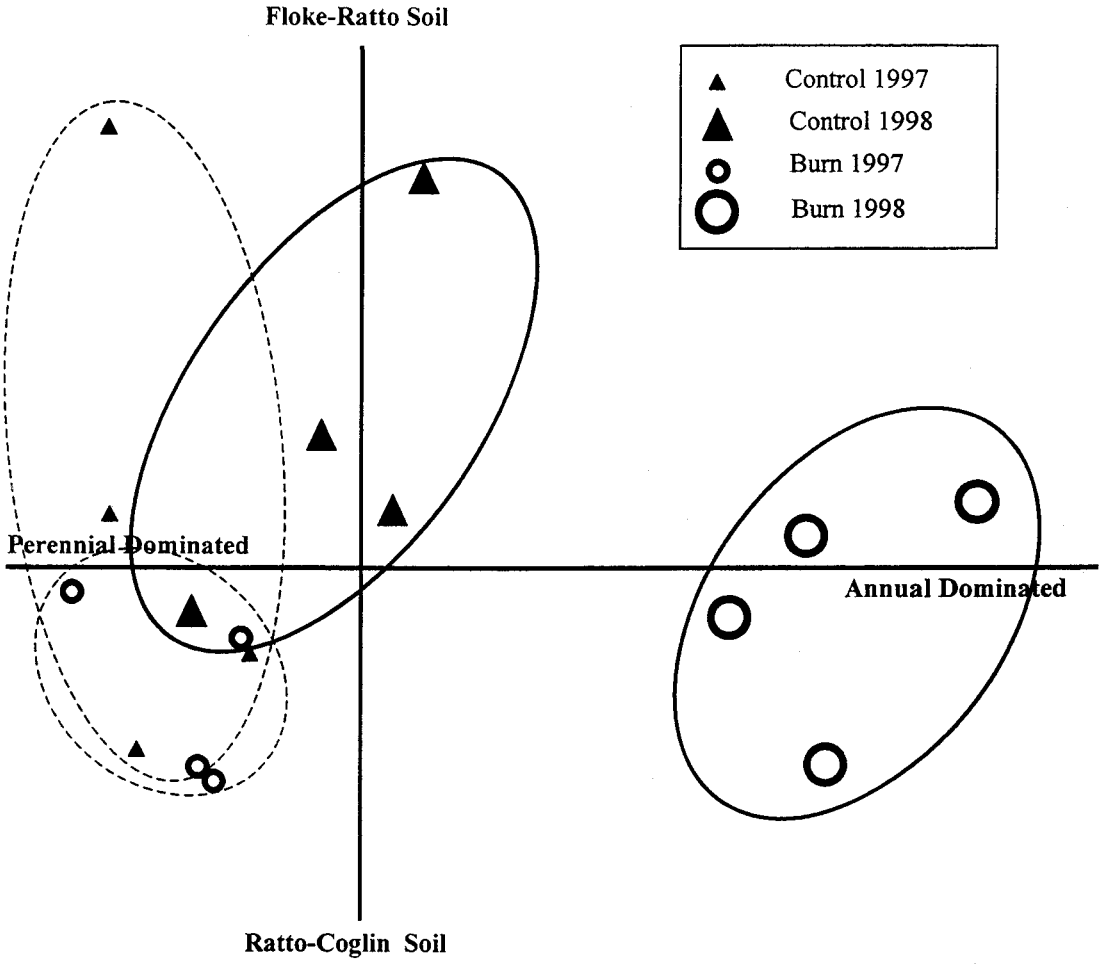

Figure 7. Location of pre- and post-burn plots in space defined by percent cover of species with principal components analysis. All 1997 plots are located toward the perennial end of the first axis. In 1998, control plots were located toward increased cover of annual species due to high precipitation; whereas burned plots were located much farther toward the annual end of the gradient due to both precipitation and prescribed burning. The plots which are higher along the second axis are those which lie closer to the boundary of the Floke-Ratto soil type and thus have a higher percent cover of species common in that soil type.

Species Diversity

No significant changes related to prescribed fire were detected in gamma and alpha diversity (Figure 8). In all study plot/year combinations, 64 genera were observed. In burned portions of treated plots 46 and 54 genera were observed before and after treatment, respectively. On burned portions of treated plots, 67 species were observed after burning. In burned and control plots combined, 59 genera and 81 species were observed versus 52 genera and 74 species in only the control plots. Thus species richness was increased by having both burned and unburned areas on the landscape.

Nine species found before prescribed fires or in control plots were not found in burned plots after fires. These species were all highly uncommon when they were observed, so their absence in burned plots after fires may not be due to elimination by burning and may be random chance. Alternatively, 5 species were found in burned plots but not in control plots. However, 3 of these were found before fires, and the other 2 were relatively uncommon and may simply not have been sampled in control plots.

Overall, 89 species were observed on the study area and 79 were classified to fire guilds (Table 3). Some infrequently encountered species were not assigned to guilds. The combined cover of the 24 species classified as strictly evaders (species with soil seed banks) increased from 0.18% cover in 1997 pre-burn plots to 0.72% in 1998 burned plots. The combined cover of the 43 species classified as endurers (species regrowing from basal tissues), although often associated with other guild classifications, declined from 0.63% in 1997 to 0.49% in 1998. Of the 5 strict invaders (species with wind transported seeds), no changes in cover due to fire were detected (0.01 in 1997 to 0.01% in 1998). The 7 species which were classified as avoiders (late-successional species with no adaptations to fire) in combination with either endurer or evader were all reduced in abundance from 3.57% to 0.01% by burning, but still persist within the burned plots.

Other Effects of Prescribed Fire

Prescribed fire also significantly reduced cover of litter by 55% (68% in 1997 to 22% in 1998) in burned plots, while only a 25% (71% in 1997 to 53% in 1998) decrease occurred in control plots ($p<0.001$).

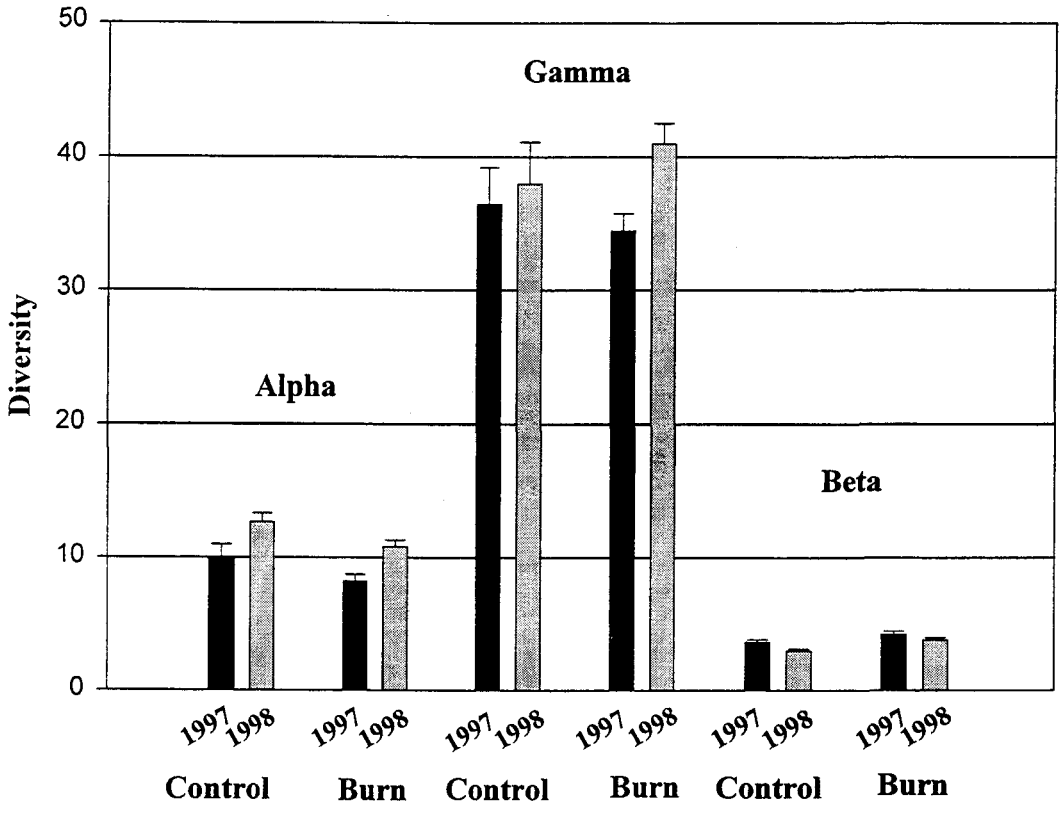

Figure 8. Mean (+SE) alpha (species transect^{-1}), gamma (species plot^{-1}), and beta (gamma/ alpha) diversity in burn and control plots during pre-treatment sampling (1997) and post-treatment sampling (1998) in a Wyoming big sagebrush ecosystem.

Table 3. Species observed in the Wyoming big sagebush experimental plots, fire guilds, and adaptations to fire.

Species	Guild	Adaptation to Fire	Additional Sources
Shrubs			
Artemesia arbuscula	Avoider/ evader	Possibly increased seeds on edge like big sagebrush	
Artemesia spinescens			
Artemesia tridentata wyomingensis	Avoider/ evader	Increased seeds on edge, prolific seeding, rapid maturation	
Atriplex confertifolia			
Atriplex nuttalli			
Atriplex spinosa	Avoider/ endurer	Basal sprout (rare)	
Ceratoides lanata	Endurer	Basal sprout	Dwyer and Pieper 1967
Gutterriza sarothae	Invader/ avoider	Windborne seed	
Tetradymia canescens	Endurer, invader	Basal sprout, windborne seed	Wright 1972
Tetradymia glabrata	Endurer, invader	Windborne seed	
Tetradymia spinosa	Endurer, invader	Basal sprout, windborne seed	
Grasses			
Agropyron smithii	Endurer	Rhizomes	
Agropyron spicatum	Endurer	Basal sprout	Conrad and Poulton 1966, Sapsis 1990
Bromus tectorum	Invader	Animal dispersed	
Elymus elymoides	Endurer/ invader	Basal sprout, wind transported seed	Wright and Klemmodson 1965
Festuca idahoensis	Endurer	Basal sprout	Conrad and Poulton 1966, Sapsis 1990
Oryzopsis hymenoides	Endurer	Basal sprout	
Poa secunda	Endurer	Basal sprout	Wright and Klemmodson 1965
Stipa thurberiana	Endurer	Basal sprout, fire enhanced flowering	Uresk et al. 1980, Wright and Klemmodson 1965
Perennial Forbs			
Agoseris glauca	Endurer/ invader	Basal sprout, windborne seed	Havlina 1995
Allium acuminatum	Endurer	Basal sprout	
Allium lemmonnii	Endurer	Basal sprout	
Antennaria dimorpha	Invader	Windborne seed	
Arabis holboellii	Endurer	Basal sprout	
Arenaria aculeata			

Table 3. Continued

Species	Guild	Adaptation to Fire	Additional Sources
Aster scopulorum	Invader	Windborne seed	
Astragalus malachus	Endurer/ evader	Basal sprout, increased flowers, seed scarification	McLean 1969, Martin et al. 1975
Astragalus obscurus	Endurer/ evader	Basal sprout, seed scarification	McLean 1969, Martin et al. 1975
Astragalus purshii	Endurer/ evader	Basal sprout, seed scarification	McLean 1969, Martin et al. 1975
Balsamorhiza saggitata	Endurer, invader	Basal sprout, windborne seed	Wright et al. 1979
Castilleja rustica	Endurer	Basal sprout	McLean 1969
Chaenactis douglasii	Invader	Windborne seed	
Crepis acuminata	Endurer/ invader	Basal sprout, windborne seed	Havlina 1995
Crepis modocensis	Endurer/ invader	Basal sprout, windborne seed, fire enhanced flowering	
Delphinium nuttalianum	Endurer/ evader	Basal sprout	
Erigeron chrysopsidis	Invader/ endurer	Windborne seed, basal sprout	
Erigeron lanatus	Invader/ endurer	Windborne seed, basal sprout	
Erigeron linearis	Invader/ endurer	Windborne seed, basal sprout	
Eriogonum cespitosum	Avoider/ invader	Winged seeds	Wright et al. 1979
Eriogonum ovalifolium	Avoider/ invader	Winged seeds	Wright et al. 1979
Haplopappus stenophyllus	Invader/ endurer	Windborne seed, basal sprout	
Lewisia rediviva	Endurer	Basal sprout	
Lomatium canbyii	Endurer	Basal sprout, fire enhanced flowering	
Lomatium donnelli	Endurer	Basal sprout	
Lomatium nevadense	Endurer	Basal sprout, fire enhanced flowering	
Lomatium vaginatum	Endurer	Basal sprout	
Lomatium watsonii	Endurer	Basal sprout, fire stimulated flowering	
Microseris troximoides	Invader/ endurer	Windborne seed, basal sprout	
Oenethera boothii	Invader/ endurer	Windborne seed, basal sprout	
Orobanche fasciculata	Endurer		
Penstemon spp.	Endurer	Basal sprout	
Phlox longifolia	Endurer/ evader	Sprout from rhizomes, fire enhanced flowering, seed bank storage	Havlina 1995
Phlox muscoides	Avoider, endurer	Weak basal sprout	
Ranunculus glaberrimus	Endurer	Basal sprout	
Senecio integerrimus	Endurer/ invader	Basal sprout, windborne seed	Havlina 1995
Tragopogon dubius	Invader	Windborne seed	Havlina 1995

Table 3. Continued

Species	Guild	Adaptation to Fire	Additional Sources
Trifolium macrocephalum			
Zygadenus venenosus	Endurer	Basal sprout	Wright et al. 1979
Annual Forbs (Stimulated by increased Nitrogen [McLendon and Redente 1991])			
Amsinckia menziesii	Evader	Soil seed storage, rapid growth	
Blepharipappus scaber	Evader	Rapid growth, windborne seed	
Camelina microcarpa			
Chenopodium spp.			
Collinsia parviflora	Evader	Rapid growth, high seed production and survival	Havlina 1995
Cryptantha circumcissa	Evader	Rapid growth, high seed production and survival	
Cryptantha intermedia	Evader	Rapid growth, high seed production and survival	
Descaurania richardsonii	Evader	Rapid growth, high seed production and survival	
Draba verna	Evader	Rapid growth, high seed production and survival	
Epilobium minutum	Evader/ Invader	Windborne seed, rapid growth, high seed production and survival	Havlina 1995
Eriastrum sparsiflorum	Evader	Rapid growth, high seed production and survival	
Eriogonum vineminum	Evader	Rapid growth, soil seed storage	
Erucastrum gallicum	Evader	Rapid growth	
Gayophytum decipiens	Evader/ invader	Rapid growth, windborne seed	
Gilia sinuata	Evader	Rapid growth, soil seed storage	Koniak 1985
Lappula spp.			
Layia glandulosa			
Lepidium perfolatum	Evader	Rapid growth	
Lithophragma bulbifera			
Lupinus pusillus	Evader	Rapid growth, seed scarification	Volland and Dell 1981, Martin et al. 1975
Mentzelia albicaulis	Evader	Soil seed storage, rapid growth	Koniak 1985
Microsteris gracilis	Evader	Rapid growth, fire enhanced flowering	
Mimetanthe pilosa	Evader	Rapid growth	
Mimulus nanus	Evader	Rapid growth	
Navarretia intertexta	Evader	Rapid growth	
Phacelia linearis	Evader	Rapid growth, fire enhanced flowering	
Phacelia lutea	Evader	Rapid growth, fire enhanced flowering	

Table 3. Continued

Species	Guild	Adaptation to Fire	Additional Sources
Plectectris macrocepha	Evader	Rapid growth	
Polemonium micranthum	Evader	Rapid growth, soil seed storage	
Ranunculus testiculatus	Evader	Rapid growth	
Scutellaria nana			

Discussion

Effects of Prescribed Fire on Sagebrush

Big sagebrush does not resprout from roots or stem bases following fire (Blaisdell 1953, Miller 1989). Burning usually kills extant sagebrush and re-invasion occurs through the chance survival of seeds or from adjacent unburned areas (Mueggler 1956). Champlin (1983) found no difference in emergence of Wyoming big sagebrush seedlings after "cool" (104°C heat exposure for 30 seconds) and "hot" (416°C for 60 seconds) fires, and controls. A greater number of reproductive shoots along burned edges would facilitate elevated seed dispersal from those edges. With reduced sagebrush competition in burned areas, seedling establishment and growth may be enhanced. I observed larger, more vigorous sagebrush seedlings in burned areas compared with control areas (seedlings 5-25 cm in height vs. 1-3 cm). Frequency of basin big sagebrush (*A.t. tridentata* Nutt.) seedlings rose from 13% before fire to 50% during the first post-fire year at John Day Fossil Beds National Monument, OR (Kauffman et al. 1997). Kauffman et al. (1997) also observed sagebrush seedlings flowering 2 years post-fire.

The elevated shoot density of sagebrush along burn edges may be caused by higher levels of nutrients as well as decreased competition and hence higher water availability. A rise in available nitrogen (NH_4 and NO_3) level occurs after both spring and fall prescribed fires and was greatest after fall fires (Kauffman et al. 1997). Miller et al. (1991) found that artificially fertilizing Wyoming big sagebrush with NH_4 and NO_3 caused greater abundance of reproductive and total shoots. Due to increased nutrient and water availability, removal of competition from one side of a plant by fire may be an important cause of increased vigor. Many aridland shrubs respond to water stress by reducing the biomass of current years growth (Kozlowski 1972). Thus increased water may elevate the shoot biomass or abundance adjacent to burned areas. In this situation, increased vigor would be expected to last until conspecifics again compete for limited water and nutrients.

Complete removal of mature sagebrush in burned areas after fire occurred in this study and has been reported elsewhere (Watts and Wambolt 1996, Fischer et al. 1997, Kauffman et al. 1997). Before fire, shrub cover on burned plots was 26%. Fire removed 100% of sagebrush cover on 47% of the area within the burned plots; the other 53% remained unburned and was likely similar to pre-fire and unburned levels. Thus, after fire, total shrub cover on the burned plots was reduced to 12%.

This reduction of sagebrush cover may bring the study plots closer to historical condition for the region. Sagebrush cover in Wyoming big sagebrush/ Thurber's needlegrass habitats in Idaho was 12%, 15%, and 21% on good, fair, and poor condition sites respectively (Tisdale et al. 1969). Some research suggests that big sagebrush cover was commonly far less than ≈25% observed in this study

(Eckert 1957, Daubenmire 1970). Eckert (1957) observed sagebrush cover values between 7 and 16% across 5 different big sagebrush and low sagebrush (*A. arbuscula* Nutt.) communities grazed by livestock at the Squaw Butte Experiment Station, Oregon. Daubenmire (1942) reported big sagebrush of 2.2% cover in a protected, ungrazed area and later (1970) reported cover that averaged 13% in 15 undisturbed, climax stands which showed no modification by livestock. These earlier estimates of sagebrush cover are lower than I observed. Ergo, pre-fire sagebrush cover on our study area was far above older estimates of cover, and may be above "natural" levels.

I classified Wyoming big sagebrush in two fire guilds, first as a fire avoider: individual plants have no means to survive fire, and sagebrush is usually one of the last species to reinvade after fire. However, I also classified sagebrush as an evader because extremely large numbers of small seeds are produced, some of which survive fire. Most seeds and seedlings are killed by high intensity fire events such as fall burns, but in our study a small percentage of seeds survived and germinated. Survival of sagebrush seedlings may be high due to the two-strata root system (deep taproot, wide fibrous roots) and the species' high content of volatile oils (unpalatable to herbivores) (Stubbendieck et al. 1992). Johnson (1958) observed a large percentage of seedlings becoming established 1 year after herbicide application. Following fire, established seedlings could potentially reproduce within 2 years (Kauffman and Sapsis 1989) to accelerate reinvasion in burned areas.

Wyoming big sagebrush also exhibits characteristics of a post-fire invader because of the greater vigor and availability of seeds along edges. These traits will enhance its recolonization of adjacent burned areas. Lightweight seeds could also allow short distance dispersal by wind. The increased reproductive and vegetative vigor of sagebrush plants along fire edges may also occur in seedlings within burned areas. It is likely that in several years the offspring of the sagebrush seedlings which germinated in the burned areas immediately after fire could form "islands" of sagebrush plants in the burned areas. Wyoming big sagebrush cover in 4-1189m^2 burned plots in Montana was not significantly different from unburned plots 30 years post-burn (Watts and Wambolt 1996). Fire return intervals which are frequent enough to exceed the capacity of sagebrush to repopulate burned areas would reduce sagebrush cover below historical levels and may also aid in the invasion of exotic species such as cheatgrass.

Grasses

The reduction in percent cover of perennial grasses caused by the prescribed fires is likely due to a decrease in plant size rather than number of individuals. Uresk et al. (1980) observed decreases in leaf length, culm length, and spike length following fire in Thurber's needlegrass, but most effects

returned to control levels within 3 years. A 23% reduction in basal area of Idaho fescue (*Festuca idahoensis* Elmer) was also measured during the first post-burn year in an ungrazed site in John Day Fossil Beds National Monument (Sapsis 1990). Mortality of perennial grasses after fire is usually low (Sapsis 1990, Uresk et al. 1980), and I observed many individuals which survived fires but were reduced in size. Although percent cover of all perennial grasses declined due to fire, frequencies of Sandberg's bluegrass and bottlebrush squirreltail, the most abundant grasses, were not significantly affected by fire. Also, density of perennial bunchgrasses was not different between burned and control plots during 1998. Experimental burning was found not to affect emergence of bottlebrush squirreltail, and to reduce emergence of Sandberg's bluegrass (Champlin 1983) which may increase the proportion of bottlebrush squirreltail in subsequent years.

Fire-enhanced flowering has been observed in many grass species (Curtis and Partch 1950, Old 1969, Sapsis 1990) and could facilitate an increase in number of grasses established in subsequent years. Reproduction of bluebunch wheatgrass (*Psuedoroegneria spicata* (Pursh) A. Love), Cusick's bluegrass (*Poa cusickii* Vasey), and Thurber's needlegrass (*Achnatherium thurberianum* (Piper) Barkworth) was enhanced by fire in south-central Washington (Uresk et al. 1980). Perennial and tall grasses would be expected to recover at least pre-treatment levels and may also increase more as measured in a basin big sagebrush ecosystem (Sapsis 1990). A 300-600% increase in basal cover of grasses was observed by third growing season after fire in a Colorado sagebrush community (Benson et al. 1991). Frequency of bluebunch wheatgrass was also noted to increase over control levels in the second post-fire year (Sapsis 1990).

Low pre-fire cover (1.5± 0.7%) and frequency (18± 3.6%) of cheatgrass (*Bromus tectorum* L.) may indicate a limited seed source and therefore reduce the effect of this species on the post-fire community. Cheatgrass in a basin big sagebrush (*A.t. ssp. tridentata*) community decreased below pre-burn levels during the first post-burn year, but returned to control levels during the second post-burn year (Sapsis 1990). Also, competition in burned areas from established perennial grasses at high densities (5.5 ±0.8 individuals/m^2) may reduce the effects of this exotic annual grass.

Forbs

Through the study period on control plots, percent cover of forbs selected by sage grouse, perennial forbs, and annual forbs increased. This is likely due to the greater precipitation in 1998. High abundance of all herbaceous vegetation coincides with high precipitation in rangeland ecosystems (Stoddart et al. 1975). The increase in species observed through years may result from 2 factors:

observer identification skills increasing through time, and encountering more rare species that were not encountered in first study year. Some noteworthy vegetative changes did occur through time. White-stemmed mentzelia was not observed, and frequency of sinuate gilia was 0.3± 0.3% during the pre-burn year. During the post-burn year, frequency of white-stemmed mentzelia was 3± 1% and 2± 0.4% and sinuate gilia was 14± 4% and 3± 1% in burned and control plots respectively. It is possible that these species have a refractory seed bank in the soil which germinates in years of extremely high moisture (such as the post-burn year), and this high germination may be amplified after fire.

The increase in overall cover of forbs caused by fire is due to the increase in cover of annual forbs. The slight increase in cover of grouse foods was caused by a drastic rise in cover of microsteris which was the only annual species in this group. Although levels of perennial forb cover remained stable through the fire event, the fire-enhanced flowering measured in Modoc hawksbeard, Lomatium, longleaf phlox, and shaggy milkvetch (Chapter 3) may facilitate an increase in perennials in the years following fire. In a nearby mountain big sagebrush community (*A.t. vaseyana*), perennial forb cover was found to have increased significantly by the second post-fire year (Pyle and Crawford 1994). Lack of differences in frequency of the abundant forb species in the community indicate that at least the abundant species, and likely others, are able to maintain relatively unchanged population levels through a fire event. No significant differences between perennial forb cover in controls and 1 year-old burns were observed in pinyon-juniper woodlands in Nevada and California, but large increases in cover of native annual forbs occurred (Koniak 1985).

Some species of Fabaceae have been documented to have seeds that are scarified by fire heat (Martin et al. 1975). Martin et al. (1975) proposed that if post-fire ground cover is scarce, and a good seed crop of milkvetch (*Astragalus spp.*) was produced before fire, populations of species within this genus may increase greatly after fire. Increases in emergence of microsteris have also been reported after "cool" burns (104°C heat exposure for 30 seconds) (Champlin 1983).

The establishment of annual species after fire was enhanced due to the availability of bare ground for establishment and the high availability of nitrogen after fire (Kauffman et al. 1997). However, when soil nutrients were not limiting, annual plants were found to dominate a sagebrush community in Colorado due to their high seed availability and growth rate (McLendon and Redente 1991). Specifically, addition of nitrogen suppressed the normal successional pathway to dominance of perennial species 3 years after plowing and enabled annual species to continue to dominate the sites through the fifth year post-plowing (McLendon and Redente 1991). It is likely that the dominance of annual species in burned areas immediately after fire is related to their short life history strategy, rapid establishment and growth rates, and the high availability of soil nitrogen.

Ecological Effects of Prescribed Fire

Prescribed fire created habitat areas with differing species compositions on the landscape. In 1997 the available gradient of species compositions is very homogenous among the 8 plots (dashed ellipses; Figure 7). In 1998, with the addition of greater precipitation, the gradient of species compositions defined by only the control plots exhibits a wider variation from the 1997 area due to the higher cover of many species. The addition of burned areas on the landscape in 1998 further increases variation in species compositions among the 8 plots from what was present in 1997 by the increases in cover of many annual species (solid ellipses; Figure 6).

Although structure was altered by the loss of sagebrush dominance, the species composition of the burned plots changed very little throughout the study, and no significant differences were observed in alpha or gamma diversity. The frequency of none of the common herbaceous species changed significantly after prescribed fire. It is likely that the detection of the less common species is due to random chance rather actual changes in the occurrence of species. The presence or absence of most species in the plots remained unchanged, but the percent cover of the species changed dramatically. Fire caused the burn plots to have higher coverages of annual forbs and sprouting herbaceous species rather than shrubs. This shift in species abundance and structure rather than composition is typical of disturbed ecosystems and follows the tolerance successional model of Connell and Slayter (1977) (Humphrey 1984).

Because sagebrush ecosystems have evolved with frequent fire (Daubenmire 1968) native plants exhibit a suite of traits which facilitate survival within the 32-100 year fire regime. Plant adaptations to fire are those which facilitate the survival of an individual or persistence of a species after fire events (Kauffman 1990). Although many annual plants may not have longer lived (>2-5 years) seeds I classified those without wind dispersed seeds as evaders. Annual species were very abundant and evenly distributed after fire, and most species do not have highly mobile seeds (D. Wrobleski, Pers. obs.). This implies a seed source in the soil before fire of which a large portion survived fire and germinated. In fact, these species did exhibit an increase in cover following fire. In general, all perennial herbaceous plants on the study area were endurers and had the ability to sprout from taproots or root crowns. The mat-forming perennial species with above-ground growth meristems (*Eriogonum spp.*, *Phlox muscoides* Nutt.) appeared to be the weakest of the endurers. The endurer species were reduced in cover by fire, but still remained an important component of the vegetative community. Avoiders are usually late-successional species which recolonize burned areas slowly in comparison with other species within the ecosystem. In our study area the longer-lived shrub species could be considered fire avoiders yet all have an additional mode of recolonization after fire. These species were most severely affected by fire. They were drastically reduced in cover. The species classified as invaders in this Wyoming big sagebrush ecosystem consist mainly of species of

Compositae and Onagraceae – families with wind dispersed seeds; however, other species such as bottlebrush squirreltail and cheatgrass also have highly efficient dispersal mechanisms. Cover of these species did not change during the first post-fire year, but would be expected to increase in later years due to high dispersal. Resisters, species which are undamaged by low severity fires, were not present in the study area.

Fire affected the most common herbaceous species (>5% frequency) and the shrub species generally in accordance with their fire guilds. The 3 most abundant shrub species, Wyoming big sagebrush, spiny hopsage, and broom snakeweed are partially classified as avoiders and were eliminated from the areas which burned with the exception of the sagebrush seedlings (thus also being classified as an evader) and the few sprouting hopsage individuals (also classified as an endurer). Blue-eyed mary, and microsteris, which were classified as evaders, both increased after burning likely due to open germination sites coupled with high seed availability and increased nutrients (Table 1). Squirreltail, Sandberg's bluegrass, wild onion, Modoc hawksbeard, dwarf yellow fleabane, desert parsley, and phlox, which were classified as endurers all persisted through the fire with no significant reduction in cover or frequency (Table 1). Squirreltail, cheatgrass, Modoc hawksbeard, and dwarf yellow fleabane, which were also classified as invaders, showed no significant increases during the first post-fire year, but wind-dispersed (or animal-dispersed) seeds may increase their abundance in the future.

Some pronounced effects of prescribed fire occurred at the burn/unburn ecotone. Immediately after the fires the wind moved large quantities of soil and ash to downwind burn edges. Increased density of reproductive and vegetative shoots along edges may partially be a result of this additional soil and ash. I also observed drastic increases in cover of grasses and forbs observed along some edges. This may be related to the high levels of soil and ash or decreased competition in the adjacent areas.

Long-Term Effects of Prescribed Fire

To estimate longer-term effects of fire on Wyoming big sagebrush ecosystems I measured six transects in a nearby 13-year-old prescribed burn area during 1998 (ca. 1985) within the same habitat and soil type. I quantified percent cover and frequency of grasses, forbs, and shrubs as described above in areas known to have burned (without live sagebrush). Cover of all perennial grasses was 13.8%, tall grass cover was 4.6%, and annual grass cover was 8.6% which was greater than both burn and control treatments indicating a recovery of grass cover in the longer term. Frequencies of bottlebrush squirreltail and cheatgrass were 50 and 82% respectively, which was greater than pre-burn or control levels. Sandberg's bluegrass frequency was 31% (lower than both treatments) possibly indicating that

the 13 year-old burn area was slightly different than the main study plots. In this area, cheatgrass was spread throughout the area (82% frequency), yet it was only abundant in localized patches and did not have a high overall cover (8.6%). Cover of grouse foods, perennial, and annual forbs was 5.2, 4.8, 10.6% respectively which was similar to control levels. It appears that after 13 years the immediate post-fire pulse in annual forbs has returned to levels similar to unburned areas. Also, 13 years post-fire, litter levels (72%) were not different from pre-burn levels (69%). Thus, after 13 years, the herbaceous components of the ecosystem have returned to pre-burn levels, but sagebrush recovery will take longer.

Effects of Fire on Sage Grouse Habitat

Although sagebrush in the Great Basin has increased through the century, sage grouse populations have not increased proportionately (Klebenow 1972). Sage grouse actually appear to seek areas where there is interspersion of habitat types (Klebenow 1972). By contrast, complete removal of sagebrush in burned areas after fire could potentially reduce nesting, hiding, and wintering cover for sage grouse (Braun et al. 1977). Sagebrush cover on our study area (and in the surrounding area) was unnaturally high (>25%) due to livestock grazing and fire suppression, there was little interspersion of other habitats in this "sea of sagebrush", yet sage grouse populations on the refuge continue to decline. Thus, it is likely that on our study area sagebrush is not a limiting factor for sage grouse populations. Reducing cover of sagebrush and increasing understory vegetation may bring the ecosystem closer to the historic conditions with which sage grouse evolved. Nesting habitat for sage grouse may not be reduced for 3 reasons: sage grouse may have evolved with lower sagebrush cover; greater than half of the burned plots did not actually burn; and higher levels of cover exist along burn edges due to elevated vigor of sagebrush. As the sagebrush seedlings within the burned areas mature and reproduce, they will begin to add sage grouse nest and hiding cover within burned areas. Additionally, with herbaceous cover along burn edges at least equal to control levels, and sagebrush cover along burn edges elevated, these edge areas may prove to be superior nesting habitat for sage grouse.

The quality of sage grouse wintering habitat after sagebrush removal treatment is directly related to the amount of sagebrush remaining (Braun et al. 1977). This prescribed fire treatment left >50% (in an irregular mosaic pattern) of the treatment area with fully intact sagebrush cover (>25%). This cover, sagebrush in the control plots, and sagebrush surrounding the study area will likely provide more than adequate wintering cover. A major danger in using prescribed fire for management of sage grouse habitat is increasing the fire frequency beyond the rate at which the sagebrush component of the ecosystem can recover. If fire return intervals became frequent enough to exceed the capacity of

sagebrush to repopulate, sagebrush cover would be reduced far below historical levels which could be very detrimental to sage grouse.

Increases in percent cover of annual forbs, will likely provide a rich forage base for pre-laying sage grouse females and young chicks. Within the burned areas, greater forb cover will enhance feeding opportunities. Several species of annual forbs were found to be primary dietary components for chicks during their first 5 weeks (Peterson 1970). If sagebrush is to be removed, interspersion of foraging and hiding cover have been suggested to provide adequate habitat for sage grouse (Braun et al. 1977). Sage grouse broods were observed feeding and roosting in strips where sagebrush had been removed by spraying, however they used adjacent unsprayed strips for shade and escape cover (Braun et al. 1977). Thus, abundant food forbs in close proximity to unburned sagebrush cover could benefit sage grouse broods by providing additional food with adequate cover. Re-introducing prescribed fire to sagebrush ecosystems with unnaturally high sagebrush cover may improve habitat quality for sage grouse by increasing forage quantity and quality, and providing greater overstory and understory cover along burn edges.

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CHAPTER 3

EFFECTS OF PRESCRIBED FIRE ON THE MORPHOLOGY, ABUNDANCE, AND PHENOLOGY OF FORBS IN WYOMING BIG SAGEBRUSH ECOSYSTEMS: IMPLICATIONS FOR ECOLOGICAL RESTORATION OF SAGE GROUSE HABITAT

Abstract

Sage grouse (*Centrocercus urophasianus* Bonaparte), once abundant in the western United States, are now being considered for listing as a threatened species. Herbaceous dicots and arthropods are a critical component of the diet of pre-laying female and young sage grouse. Fire suppression and other land uses have likely reduced abundance of these species in rangeland ecosystems. Reintroducing fire would decrease shrub overstory, and create other conditions that may favorably affect herbaceous dicot species and arthropod numbers. In September, 1997 prescribed fire was applied to 4 of 8 randomly assigned Wyoming big sagebrush (*Artemesia tridentata wyomingensis*) study plots to examine the first-year effects of fire on morphology, abundance, and phenology for 9 dicot species. Fire-enhanced reproduction was measured for 5 of 9 species examined. Burning resulted in significantly greater mean numbers of racemes and mean flowers/ raceme in shaggy milkvetch (*Astragalus malachus*) (9 racemes in burn vs. 6 in control; 23 flowers/ raceme in burn vs. 21), greater mean numbers of flowers in microsteris (*Microsteris gracilis*) (57 vs. 13), greater mean number of umbels and umbelletts in Nevada desert parsley (*Lomatium nevadensis*) (4 vs. 2; and 59 vs. 31 respectively), greater mean numbers of flower heads in Modoc hawksbeard (*Crepis modocensis*) (32 vs. 21), and greater mean number of flowers cm^{-3} in longleaf phlox (*Phlox longifolia*) (0.11 vs. 0.06). Burning also resulted in greater mean crown volume of Modoc hawksbeard (7,085 vs. 4,179cm^3) and shaggy milkvetch (2,854 vs. 1,761cm^3), and lower crown area of low pussytoes (20 vs. 37cm^2). The period of active growth was extended in burned plots; all measured species remained green and succulent later into the growing season ($P< 0.01$). In addition, Modoc hawksbeard and Nevada desert parsley flowered 12 – 14 days earlier in burned plots. Fire had a significant negative affect on low pussytoes (*Antennaria dimorpha*) by reducing frequency, density, and relative abundance. Frequency and relative abundance of longleaf phlox were also significantly lower in burned plots. The abundance of other species was unaffected by fire. Fire enhanced flowering could facilitate an increase in dicot abundance in subsequent years following fire if seed production was enhanced. From 1997 to 1998,

average number of ants trap^{-1} increased by 116 in burned plots and only 6 in control plots. Abundance of beetles and other ground dwelling arthropods were unaffected by fire. The greater availability of plant reproductive parts, larger plants, longer period of photosynthesis, and increases in ants caused by prescribed fire would increase available foods for sage grouse.

Introduction

Forbs (herbaceous dicots) are seasonally important components of sage grouse (*Centrocercus urophasianus* Bonaparte) diets and a lack of available forbs has even been suggested to be a cause of decreased productivity in sage grouse populations (Crawford and Lutz 1985, Barnett and Crawford 1994, Drut et al. 1994b). Dicots such as mountain dandelion (*Agoseris spp.*), Everlasting (*Antennaria spp.*), milkvetch (*Astragalus spp.*), hawksbeard, (*Crepis spp.*), buckwheat (*Eriogonum spp.*), wild lettuce (*Lactuca spp.*), pepperweed (*Lepidium spp.*), desert parsley (*Lomatium spp.*), microsteris (*Phlox gracilis* Greene), phlox (*Phlox spp.*), dandelion (*Taraxacum spp.*), clover (*Trifolium spp.*), and ground dwelling arthropods such as beetles and ants are key dietary components of sage grouse in Wyoming big sagebrush (*Artemesia tridentata wyomingensis* Beetle & Young) and low sagebrush (*Artemesia arbuscula* Nutt.) habitats (Rogers 1964, Peterson 1970, Barnett and Crawford 1994, Drut et al. 1994a). Leaves and flowers of these and other dicots are likely important components of the diet for pre-laying females and chicks (Peterson 1970, Barnett and Crawford 1994, Drut et al. 1994a) because they contain higher amounts of crude protein, calcium, and phosphorus than sagebrush (*Artemesia spp.*) (Barnett and Crawford 1994). Furthermore, the abundance of forbs have been associated with sage grouse productivity by affecting the dietary intake and hence the growth and survival of chicks (Drut et al. 1994a).

While the importance of these dicots have been demonstrated for sage grouse diets, little is known about the ecology of these species. The response of these common rangeland species to natural ecosystem processes such as fire, and the potential of these vegetative responses to affect obligates of sagebrush ecosystems such as sage grouse, have not been quantified in an experimental context.

Human land uses, particularly livestock overgrazing and fire suppression have resulted in longer fire return intervals in sagebrush ecosystems, leading to increasing woody species dominance (e.g. sagebrush and western juniper (*Juniperus occidentalis* Hook.) (Kauffman and Sapsis 1989, Miller et al. 1998). This has led to a decrease in understory forbs and grasses (Miller 1989). Big sagebrush, the dominant woody species, does not sprout and is readily killed by low intensity fires (Blaisdell 1953, Miller 1989). The reduction of sagebrush following fire enhances production of understory species

through increases in available water, light, and nutrients (Young and Evans 1978, Kauffman et al. 1997).

I hypothesized that prescribed fire within sagebrush ecosystems could enhance sage grouse habitat by increasing the abundance of dicots and arthropods. I also hypothesized that the morphology and phenology of dicot species may be positively affected by prescribed fire. Fire may increase abundance of dicots by seed scarification, increasing microsites favorable for germination and establishment, and decreasing competition with the shrub overstory (Gill 1981, Kauffman 1990). The pulse of nutrients, water, and sunlight following fire have been found to influence plant morphological characteristics such as crown area and crown volume (Daubenmire 1968, Sapsis 1990, Kauffman et al. 1997). Also, in many species, fire changes the reproductive rate of plants by increasing the number of flowers or inflorescences (Curtis and Partch 1950, Stone 1951, Pyke 1983, Kauffman 1990). This could enhance forage quality for sage grouse due to higher nutritional value in reproductive plant parts (Holochek et al. 1989). Increases in available nitrogen and phosphorus cations in ash following fire may also affect plant morphology, and phenology during the initial post-fire period (Kauffman et al. 1997). These changes may affect phenology of these key forbs resulting in longer periods of succulence during a growing season (Curtis and Partch 1948, 1950, Stone 1951, Daubenmire 1968, Pyke 1983).

Sage grouse food availability in uplands becomes limiting as vegetation senesces in late summer and birds move into more mesic areas (Fischer et al. 1996). Thus, increasing succulent foods in uplands may positively affect availability of sage grouse foods. Overall, prescribed fire has the potential to increase food abundance for sage grouse by increasing size, abundance, and the length of time available of herbaceous dicot species important in their diet.

The pulse of nutrients, water, and sunlight, and possibly increased herbaceous component promoted by fire may also increase arthropod abundance (Drut et al. 1994a). Ground-dwelling arthropods were found to be important in the diet of young sage grouse chicks (Rasmussen and Griner 1938, Rogers 1964, Peterson 1970, Drut et al 1994a). Chicks which were deprived of insect material had restricted growth or died within 10 days (Johnson and Boyce 1990). Sage grouse chick selection of arthropod food material is thought to be principally due to the order of availability on the landscape (Rasmussen and Griner 1938). Enhancing arthropod abundance following fire would further amplify the value of burned areas to sage grouse.

The U.S. Fish and Wildlife Service has been working toward the ecological restoration of rangeland ecosystems at Hart Mountain National Antelope Refuge in southeastern Oregon. Livestock grazing was reduced until 1991 when it was completely eliminated. This has had profound positive effects on the understory grasses and forbs in the sagebrush ecosystems (Coggins 1999). To continue this restoration effort in recent years, the USFWS has added active restoration practices in the form of prescribed fire to the highly successful passive restoration program. Returning fire to sagebrush

ecosystems could restore these areas to the historic balance of ecosystem components which supported an abundance of wildlife species.

Our research objectives were to quantify the effects of prescribed fire on the morphology (size and number of flowers); abundance (frequency, density, relative abundance); and phenology (length of active aboveground growth and flowering time) of 9 selected herbaceous dicot species that are important in the diet of pre-laying sage grouse females and young chicks. Secondly, I quantified the effects of prescribed fire on abundance of ground-dwelling arthropods.

Study Area

Plant response to prescribed fire was evaluated on 4 burned and 4 control plots in a Wyoming big sagebrush ecosystem. Four plots were chosen randomly for prescribed fire treatment. Plots were ≅400ha in size and located in the northeastern portion of Hart Mountain National Antelope Refuge, OR (Figure 1). Elevation of the study plots ranged from 1,550 m to 1,615 m with level topography. Soils were a cobbly clay-loam of the Ratto-Coglin complex, Ratto series (SCS 1991). Mean temperature between March and July on the study area was 13°C. Mean annual precipitation at refuge headquarters was 29 cm (Drut et al. 1994b). Precipitation was 24.9 and 45.6 cm in 1997 and 1998 respectively (U.S.F.W.S. Unpubl. Data). Study plots have not been grazed by livestock since 1991, and not burned for >50yrs (U.S.F.W.S. Unpubl. data). Dominant grasses in the study plots were bottlebrush squirreltail (*Elymus elymoides* Rafin.), and Sandberg's bluegrass (*Poa sandbergii* Vasey). Small communities dominated by low sage (*Artemesia arbuscula* Nutt.), basin big sagebrush (*A.t.* ssp. *tridentata*), or grasses were found within the study areas but were not sampled.

Methods

Prescribed Fire Treatment

Before, during, and after ignition of prescribed fires, information about weather, fuels, and fire behavior were collected. Weather data (temperature, relative humidity, wind speed, cloud cover, and

precipitation) were collected at the burn plots during prescribed burning with a belt weather kit. Pre-fire understory biomass was measured by clipping 25– 20x50cm micro-plots in each plot, drying at 50°C and weighing the material. This was repeated after the fires to obtain post-fire understory biomass. Understory fuel consumption was calculated as the percentage of biomass lost due to fires. Pre-fire biomass of Wyoming big sagebrush in each burn plot was determined with the following equation:

$$\text{Total Fuel Biomass (kg ha}^{-1}) = -2419.043 + 93.548\,(L) + 62.537\,(H)$$

Where (L) = the line intercept canopy cover of Wyoming big sagebrush and (H) = the height of sagebrush in cm (Champlin 1983). Fuel moisture of the understory as a proportion of dry weight was measured by clipping and drying 10 random, 20x50 cm samples of understory in each plot immediately before ignition of fires. Ten-hour moisture sticks were used to estimate moisture of dead 10-hour fuels. Flame height, flame length, flame depth, rate of spread, and residence time were measured by observation during each fire. Line intercept was used to measure percent area burned along 5 transects beginning at a random starting point and crossing the plot in a random direction on 1"/1000' infrared aerial photos (Brower et al. 1990). Because sage grouse require sagebrush interspersed with open patches on the landscape (Braun et al. 1977), the number of burned/ unburned edges linear km^{-1} in treatment plots were quantified along 15 similar transects.

Morphology of Dicots Selected by Sage Grouse

Shaggy milkvetch (*Astragalus malachus* Gray), Pursh's milkvetch (*Astragalus purshii* Dougl.), Canby's lomatium (*Lomatium canbyi* Coult. & Rose), Nevada desert parsley (*Lomatium nevadense* (Wats.) Coult. & Rose), Watson's desert parsley (*Lomatium watsonii* Coult. & Rose), microsteris (*Phlox gracilis* Greene), longleaf phlox (*Phlox longifolia* Nutt.), low pussytoes (*Antennaria dimorpha* (Nutt.) T. & G.), and Modoc hawksbeard (*Crepis modocensis* Greene) have been identified as important foods for sage grouse within the study area (Barnett and Crawford 1994, Drut et al. 1994a). These species were also used to evaluate morphological response to prescribed fire because they were frequently encountered in plots before the prescribed fires.

To quantify the effects of prescribed fire on morphology of the selected species, 25 individuals of each species were measured upon being encountered along random transects in each control and burned plot. Individuals of each species were measured during the peak of growth within the growing season (when most plants of the species were in full flower). For each individual, number of

inflorescences (heads, umbels, or racemes) and number of flowers (solitary flowers or umbelletts) were counted. Maximum height from the ground (if the species was not prostrate) and elliptical crown area were measured. Crown area was calculated with the formula:

$$\text{Area} = (w1 * w2 * \pi) / 4$$

Where W1 is the maximum crown diameter, and W2 is the perpendicular diameter at its midpoint (Case and Kauffman 1997). Crown volume was calculated as the product of crown area and height. Due to varying growth forms, not all morphological variables were measured for each species (e.g. longleaf phlox has only solitary flowers, not inflorescences). I also calculated number of flower heads cm^{-2}, and number of flowers cm^{-3} for low pussytoes and longleaf phlox, respectively.

To detect if burning caused an effect on plant morphology, I selected 2-3 dependent variables per species. These variables most accurately represented the species' reproductive and vegetative growth form (e.g. for shaggy milkvetch: number of racemes, number of flowers $raceme^{-1}$, and crown volume). Because variables were related and likely shared variance, fire effects on morphology were initially compared simultaneously between treatments for each individual species with multivariate analysis of variance with α=0.20 (MANOVA) (Tabachnick and Fidell 1996). Number Cruncher Statistical Systems (NCSS) (Hintze 1997) was used for data screening and Statistical Analysis Systems (SAS) (SAS Institute Inc. 1990) was used for analysis. To determine how the effects of each of these dependent variables affected the overall result for that species, analysis of variance (ANOVA) on each individual variable was used with α=0.10 to reduce type II error rate.

Abundance of Dicots Selected by Sage Grouse

The initial post-fire abundance of dicot species prevalent in sage grouse diets was measured during the 1998-growing season. Fifty randomly placed 20-m transects were sampled in all plots. Along transects, I placed 10 equidistantly spaced $1m^2$ micro-plots, with 10- 20x50-cm nested plots within them and recorded frequency, density, and relative abundance of all dicot species selected for by sage grouse. Frequency was percent presence of the species in the larger microplots along a transect. Density of each species was measured by counting the number of individuals within the $1m^2$ micro-plots. Density of each species within microplots was totaled within each transect to yield the number of plants $10m^{-2}$. Relative abundance was calculated for each species in a transect by scoring presence in

the larger plot as 1, and presence in the smaller plot as 10 due to the relative size of the plots and totaling all scores within a transect (maximum=100) (Smith et al. 1987).

To detect differences in overall plant abundance between burn and control plots, a 2x9 factorial MANOVA was performed with frequency, density, and relative abundance (overall abundance) as dependent variables because these variables are likely affected simultaneously by fire (Tabachnick and Fidell 1996). Independent variables (factors) were treatment (prescribed fire/control) and the 9 selected dicot species. A second similar 2x10 MANOVA was then performed on treatment and the 10 other sage grouse food species which were less common on the study area. These are arcane milkvetch (*Astragalus obscurus* Wats.), ovalleaf buckwheat (*Eriogonum ovalifolium* Nutt.), broom buckwheat (*E. vineminum* Dougl.), mat buckwheat (*E. cespitosum* Nutt.), Donnell's lomatium (*Lomatium donnellii* Coult. & Rose), nine-leaved desert parsley (*L. triternatum* (Pursh) Coult. & Rose), Broad-sheathed lomatium (*L. vaginatum* Coult. & Rose), tapertip hawksbeard (*Crepis acuminata* Nutt.), mountain dandelion (*Agoseris glauca* (Pursh) Raf.), and false agoseris (*Microseris troximoides* Gray). After the initial MANOVAs comparing the 3 dependent variables by treatment and species, another series of MANOVAs compared the 3 dependent variables by treatment for each of the 19 species separately. The less common dicot species were not tested further because of infrequent occurrence on some or all plots and thus reduced sample sizes.

Analysis proceeded further for the 9 selected dicot species. If I detected significant treatment effects in frequency, density, and relative abundance simultaneously tested at the species level, effects of fire on individual dependent variables were then tested with ANOVA. MANOVA tests were considered significant at α=0.20 and ANOVA tests were significant at α=0.10 to reduce the chance of a type II error.

Phenology of Dicots Selected by Sage Grouse

To determine if dicots flowered earlier or remained green and succulent longer in burned areas phenological response was measured on the selected dicot species. At a randomly selected starting point for each plot, a random direction was selected and a transect was established. Along these transects I assigned a phenological stage to 10-20 individual plants of each species (Table 4). Phenological stages were developed by field observation of the dicot species during preliminary sampling. Individual plants were selected as encountered along the transect. If a transect did not yield a sufficient number of individuals the process was repeated within that plot. Transects were resampled every 12 – 20 days beginning 17 April and ending when the selected species had senesced on 29 July.

Table 4. Phenological stages used to assess effects of prescribed fire on herbaceous dicot species in a Wyoming big sagebrush ecosystem.

Number	Phenological Stage	Criteria
1	Vegetative	Green leaves present, but no reproductive organs present
2	Pre-flower	Flower organs available, > 50% flowers on the individual pre-anthesis
3	Flower	Majority of flowers (>50%) in anthesis
4	Post-flower	>50% of flowers post-anthesis, photosynthetic (green or succulent) material available on leaves or stems
5	Senesced	Plants dry, no photosynthetic material available

To examine the effects of prescribed fire on phenology of dicots, species phenology in burn and control plots was first assessed graphically. To test the specific hypothesis that selected species remained green and succulent longer in burned plots than in control plots, I used only data from the latest sampling period in which some individuals of a species remained succulent. This sampling period occurred on either 29 June, 12 July, or 28 July, depending on the phenology of the species. For each species a 2x2 contingency table was formed of the final phenological stages (post-anthesis and senescence as rows) by treatment (burn and control as columns) and independence was tested with the Fisher exact test (Zar 1996:540).

To determine whether species flowered earlier in burned plots, data were plotted during the time period when a large proportion (>25%) of the sampled plants were flowering (in the pre-flower, flower, or post-flower phenological stages) and compared between treatments.

Proportion of Population Flowering

To determine what proportion of the population of each species would flower, the proportions of plants in pre-anthesis, anthesis, or post-anthesis phenological stages (individuals which would flower) versus those in the vegetative stage (individuals which would not flower that year) (Table 4) were compared between treatment and control plots. Because all annual plants were observed flowering, the proportion of plants flowering was only compared with perennial species. This was done with data from sampling periods only on 19 May and 3 June. By this time all mature plants showed distinct evidence of flowering and immature individuals did not. Differences in the proportion of individual plants reproducing in burned and control plots were tested with confidence intervals

calculated at the 90% level (Daniel 1995). If confidence intervals included zero, no differences existed between treatments in proportion of plants in the population of each species reproducing during the first post-fire year.

Arthropod Abundance

Ground dwelling arthropod abundance was measured within each of the treatment and control plots in both the pre- and post-treatment years. Four traps, consisting of plastic cups (described by Morill 1975), were inserted into the soil in a 1-m^2 area at 15 locations within each study plot. Traps were placed in a systematic grid pattern throughout each plot. Trapping occurred beginning 1 June, the mean sage grouse hatch date at which time arthropods are used most heavily by sage grouse (Rogers 1964, Peterson 1970, Drut et al. 1994a). During post-burn sampling, traps were placed in unburned controls and only in burned areas of treatment plots. At the end of the 7-day trapping period arthropods were classified to order.

Abundance of coleoptera (beetles), hymenoptera (ants), and other arthropods were used as dependent variables and compared between prescribed fire treatment and control for pre- and post-fire years with MANOVA (α=0.20). The YEAR term indicated differences between years, the PLOT term indicated pre-existing differences between treatment and control plots, and the YEAR X PLOT interaction (i.e. differing year effect by treatments) indicated a fire treatment effect. ANOVA was then used to determine which dependent variables contributed to significance (α=0.10).

Results

Prescribed Fire Treatment

The prescribed fire plots were ignited with a heli-torch September 23-28, 1997 utilizing strip-head or ring-fire ignition patterns (Martin 1990). Ambient temperature during fires ranged from 19° to 28°C, relative humidity ranged from 17 to 24%, Wind speed ranged from 6.4 to 9.7km h^{-1}, cloud cover

was <10%, and there had been no precipitation for > 2 weeks. Pre-fire understory biomass in the burned plots ranged from 1,260-1,820 kg ha^{-1} and overstory biomass was 3,444± 106 kg ha^{-1}.

In the post-fire mosaic there were 27± 2.0 edges linear km^{-1}. Thus, along a transect, a burn/unburn edge was crossed every 37m. Approximately 47% (range=36-62%) of the area within the treated plots was burned. Within burned areas all sagebrush biomass was consumed. Thus throughout the treatment plots 1619± 50 kg ha^{-1} of sagebrush remained after fire. Understory consumption was 80± 8% within burned portions of treatment plots, and 37± 4% throughout the entire area of the burned plots. Understory fuel moistures for the dead herbaceous vegetation ranged from 4.4-6.5%; moisture of 10-hour dead fuels ranged from 5.5-8.0%. Flame height ranged from 2-3.7m, flame length ranged from 2-4.4m, flame depth ranged from 2-7.8m, rate of spread ranged from 4.6-12 m/min, and residence time ranged from 0.6-2.6 minutes. Mean estimate of Byram's fireline intensity was 1,321 kW m^{-1}, reaction intensity was 302 kW/m^2 (Alexander 1982).

Effects of Prescribed Fire on Morphology of Dicots

Reproductive and vegetative growth was significantly enhanced for microsteris (p=0.005), Modoc hawksbeard (p=0.024), Nevada desert parsley (p=0.002), shaggy milkvetch (p=0.160), longleaf phlox (p=0.148), and *Lomatium spp.* (p=0.050). Reproductive and vegetative growth was significantly lower in burned plots for low pussytoes (p=0.176).

Reproductive effort, measured by the number of inflorescences (heads, umbels, or racemes), was significantly greater in burned plots for Modoc hawksbeard (burn=32± 2, control=21± 4; p=0.07), Nevada desert parsley (burn=3 ± 0.5, control=2± 0.1, p=0.06), all *Lomatium spp.* (burn=4± 0.7, control=2± 6.7; p=0.02), and shaggy milkvetch (burn=9± 0.8, control=6± 0.6; p=0.02) (Figure 9). Number of flowers was significantly greater in burned plots for microsteris (burn=57± 11, control=13± 1; p=0.006), Nevada desert parsley (burn=59± 4.5, control=31± 2.3; p=0.005), and *Lomatium spp.* (burn=31± 11.6, control=17± 5.4; p=0.09) (Figure 10). For longleaf phlox, the number of flowers cm^{-3} of plant volume was significantly greater (burn=0.11± 0.01, control=0.06± 0.01; p=0.02) in burned plots, also, shaggy milkvetch had greater numbers of flowers $inflorescence^{-1}$ in burned plots than in control plots (burn=24± 0.5, control=20± 0.7; p=0.03).

In burned plots, crown volume was significantly greater for Modoc hawksbeard (burn=7,085± 620, control=4,179± 208; p=0.04) and shaggy milkvetch (burn=2,854± 339, control=1,761± 415; p=0.09) (Figure 11). Crown area was significantly lower for low pussytoes in burned plots (burn=21± 3 control=37± 8; univariate ANOVA p=0.09) (Figure 12).

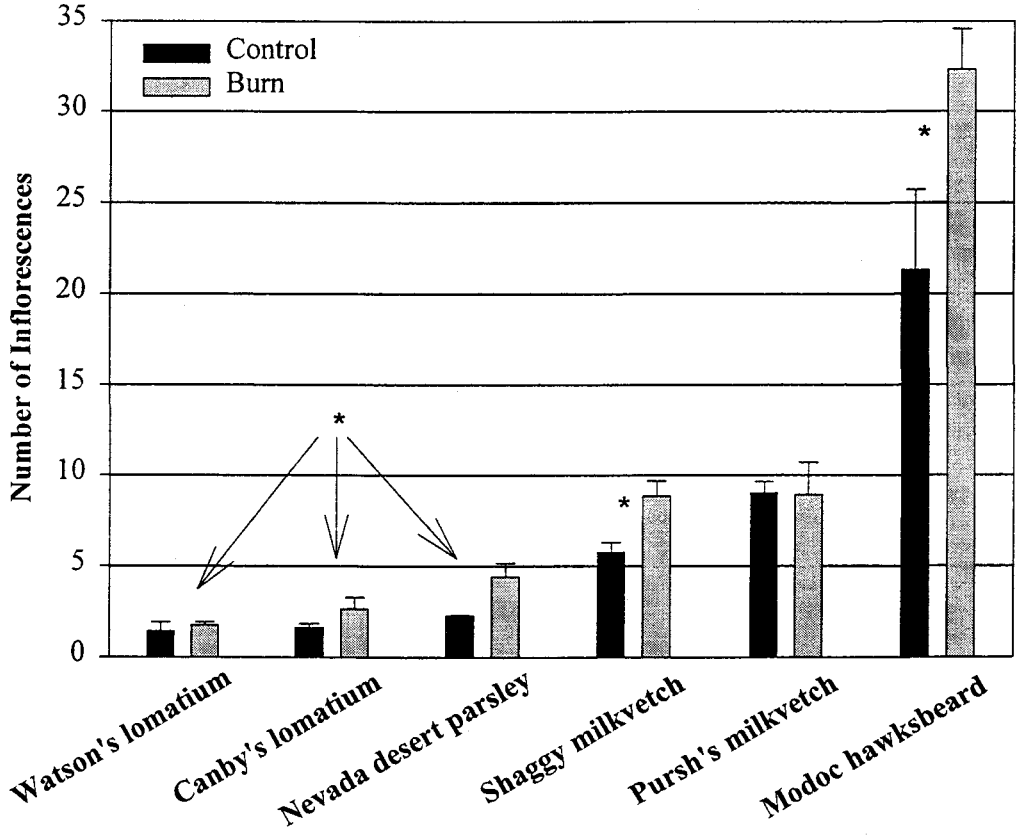

Figure 9. Mean number of inflorescences (umbels, racemes, or flower heads) per individual (+SE) of Watson's lomatium, Canby's lomatium, and Nevada desert parsley, shaggy milkvetch, Pursh's milkvetch, and Modoc hawksbeard in burn and control plots. All species are depicted on which the number of inflorescences was considered a valid measure of their reproductive effort. Number of inflorescences was measured during the period of most active flowering for each species during the 1998 growing season after prescribed fires in September, 1997. An * indicates a significant difference at α=0.10.

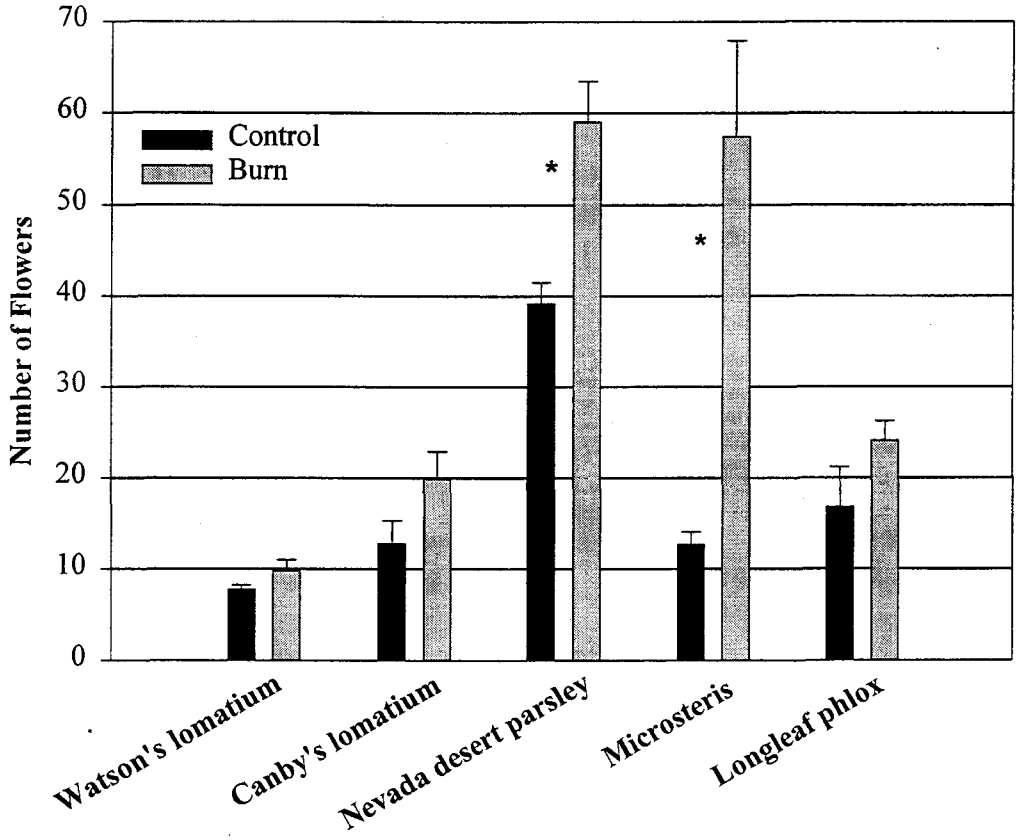

Figure 10. Mean number of flowers (or umbelletts) per individual (+SE) of Watson's lomatium, Canby's lomatium, Nevada desert parsley, microsteris, and longleaf phlox in burn and control plots.. All species are depicted on which the number of flowers was considered a reliable measure of their reproductive effort. Number of flowers was measured during the period of most active flowering for each species during the 1998 growing season after prescribed fires in September, 1997. An * indicates a significant difference at α=0.10.

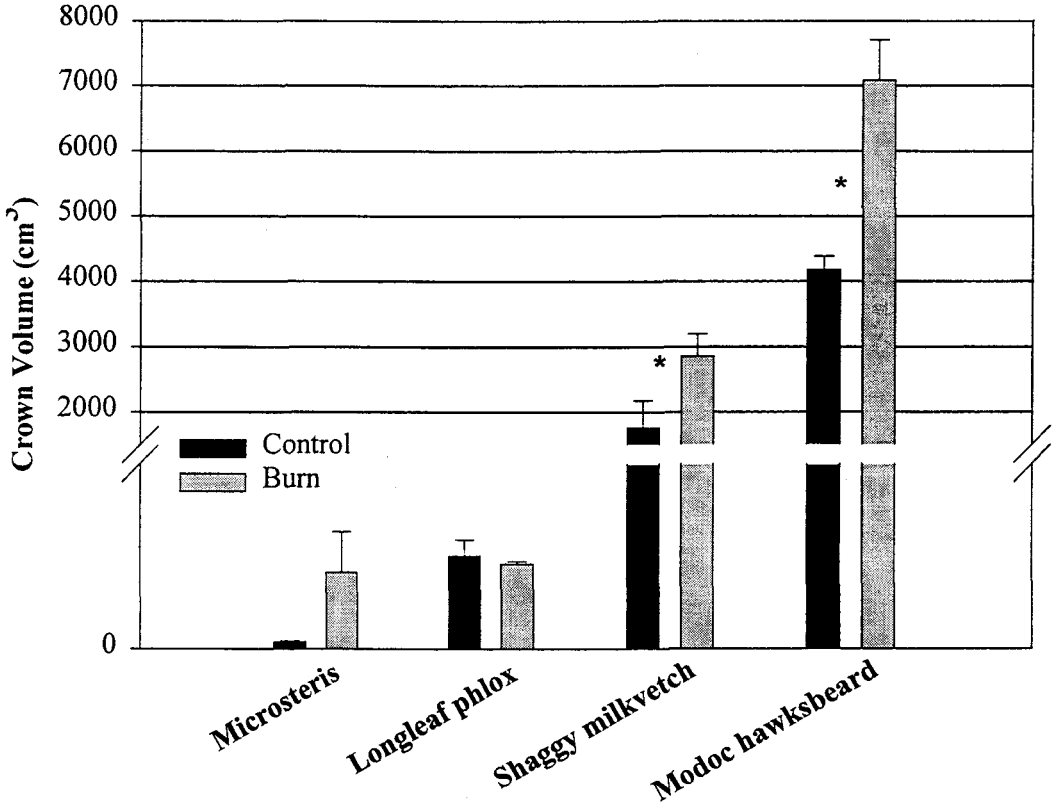

Figure 11. Mean crown volume per individual (+SE) of microsteris, longleaf phlox, shaggy milkvetch, and Modoc hawksbeard in burn and control plots. All species are depicted on which the crown volume was considered an appropriate measure of their vegetative effort. Crown volume was measured during the period of most active flowering for each species during the 1998 growing season after prescribed fires in September, 1997. An * indicates a significant difference at α=0.10.

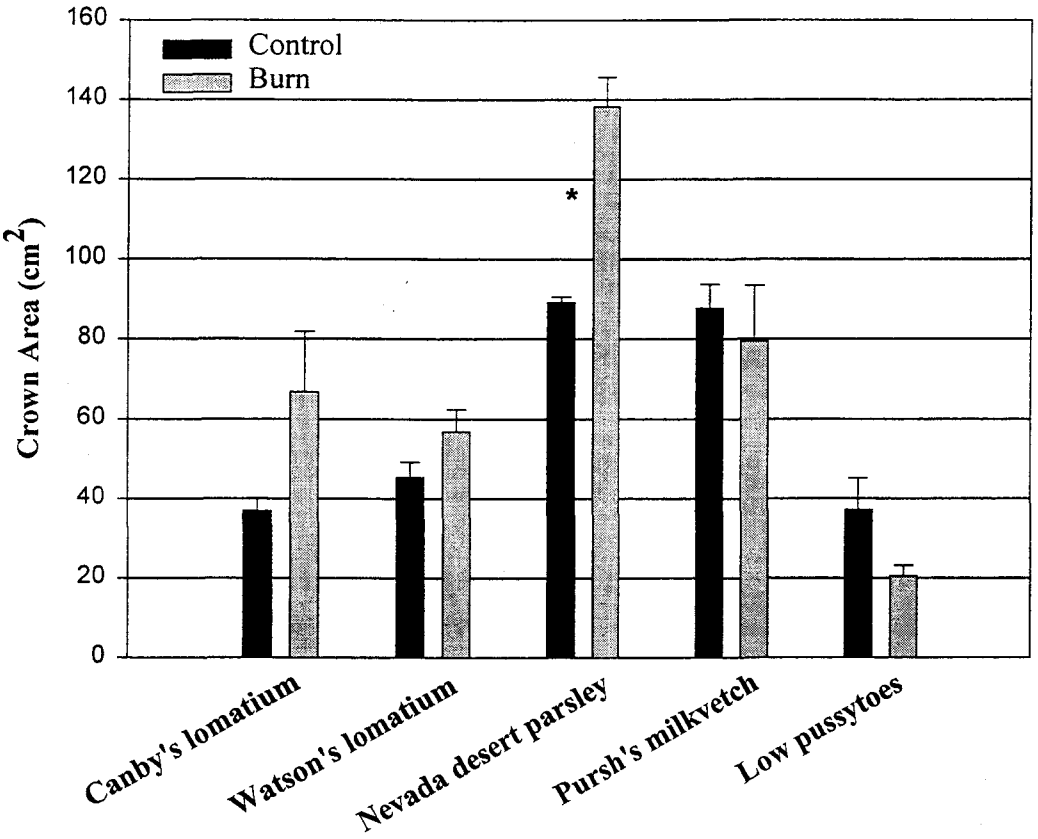

Figure 12. Mean crown area per individual of Canby's lomatium, Watson's lomatium, Nevada desert parsley, Pursh's milkvetch, and low pussytoes in burn and control plots. All species are depicted on which the crown area was considered a valid measure of their vegetative effort. Crown area was measured during the period of most active flowering for each species during the 1998 growing season after prescribed fires in September, 1997. An * indicates a significant difference at α=0.10.

Effects of Prescribed Fire on Abundance of Dicots

Overall abundance of low pussytoes (p=0.008), Modoc hawksbeard (p=0.059), and longleaf phlox (p=0.164) was lower in burned plots (Table 5, Figure 13, 14, 15). Specifically, frequency (burn=1± 0.3%, control=8± 1.8%; p=0.01), density (burn=0.2± 0.1, control=1± 0.4; p=0.03), and relative abundance (burn=0.4± 0.1, control=2± 0.7; p=0.04) of low pussytoes was significantly lower in burned plots. Relative abundance of Modoc hawksbeard was significantly lower in burned plots (burn=11± 2.7, control=24± 6.2; p=0.09). However, frequency of Modoc hawksbeard before prescribed fires during 1997 was lower in burned plots than control plots (5.5 vs. 16.8% Table 1). Frequency (burn=24± 4.5, control=41± 5.8; p=0.06) and relative abundance (burn=12± 2.1, control=24± 4.0; p=0.04) were also lower in burned plots for longleaf phlox. No other significant differences between treatments existed in frequency, density, and relative abundance of the selected dicot species (p>0.10).

Abundance was significantly lower in burned plots when overall abundance of the 10 less abundant sage grouse species were combined (p<0.001). However, only tapertip hawksbeard (p<0.001) and ovalleaf buckwheat (p<0.002) were significantly lower in abundance in burned plots (Table 5).

Effects of Prescribed Fire on Phenology of Dicots

As expected, the differences in phenology were strong through time and among species during the growing season; however, the burn treatment caused several changes in phenology (Figure 16). Prescribed burning extended the period of active photosynthesis for all species (P<0.001 for each species). Within each of the selected species, the percent of green and succulent plants immediately before senescence (29 June for Canby's lomatium, 28 July for Modoc hawksbeard and longleaf phlox; and 12 July for all other species) was greater in burned than control plots (Figure 16).

In Modoc hawksbeard and Nevada desert parsley reproductive parts appeared in a large proportion (>25%) of sampled plants in burned plots earlier than control plots (19 May in burn, 2 June in control; and 17 April in burn, 29 April in control respectively) (Figure 17). Reproductive parts were present on a large proportion (>25%) of sampled plants in burn plots but not control plots during the final sampling period for each species except Pursh's milkvetch and longleaf phlox (Figure 16). Burning also significantly increased the proportion of plants in the population flowering during the first post-fire growing season for Modoc hawksbeard (41% in burn vs. 25% in control) and longleaf phlox (65% in burn vs. 45% in control) (Table 6).

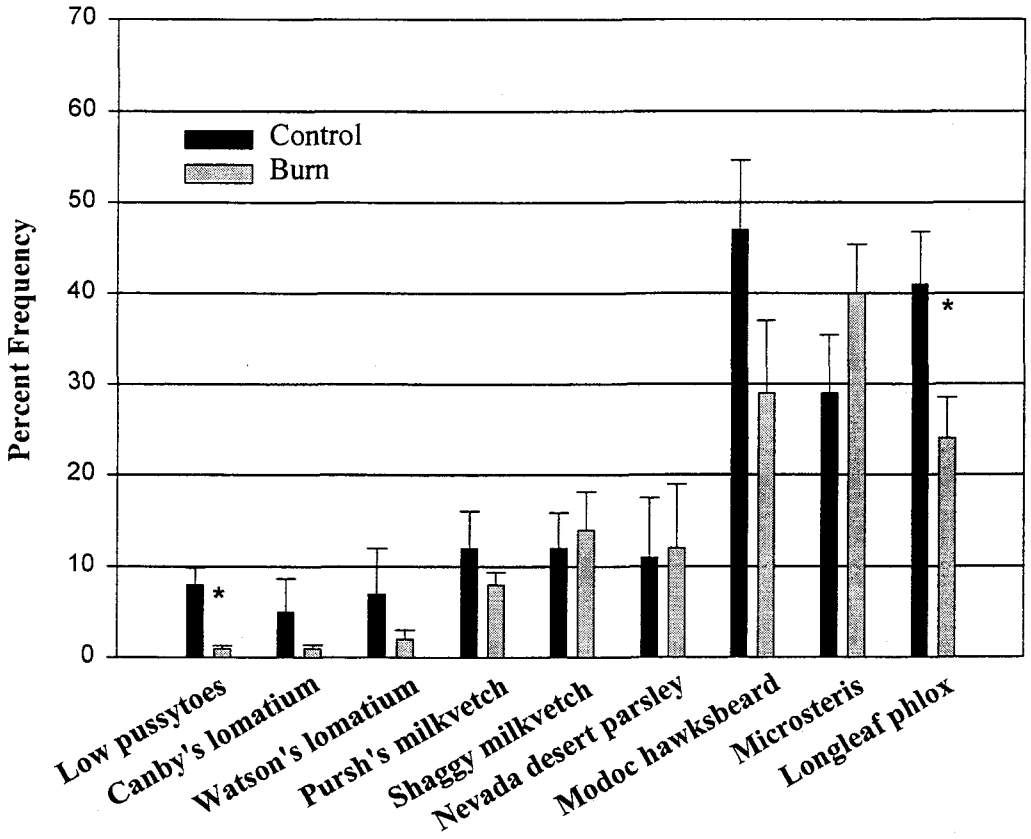

Figure 13. Percent frequency (+SE) of selected herbaceous dicot species in control and burn plots within the Wyoming big sagebrush ecosystem.

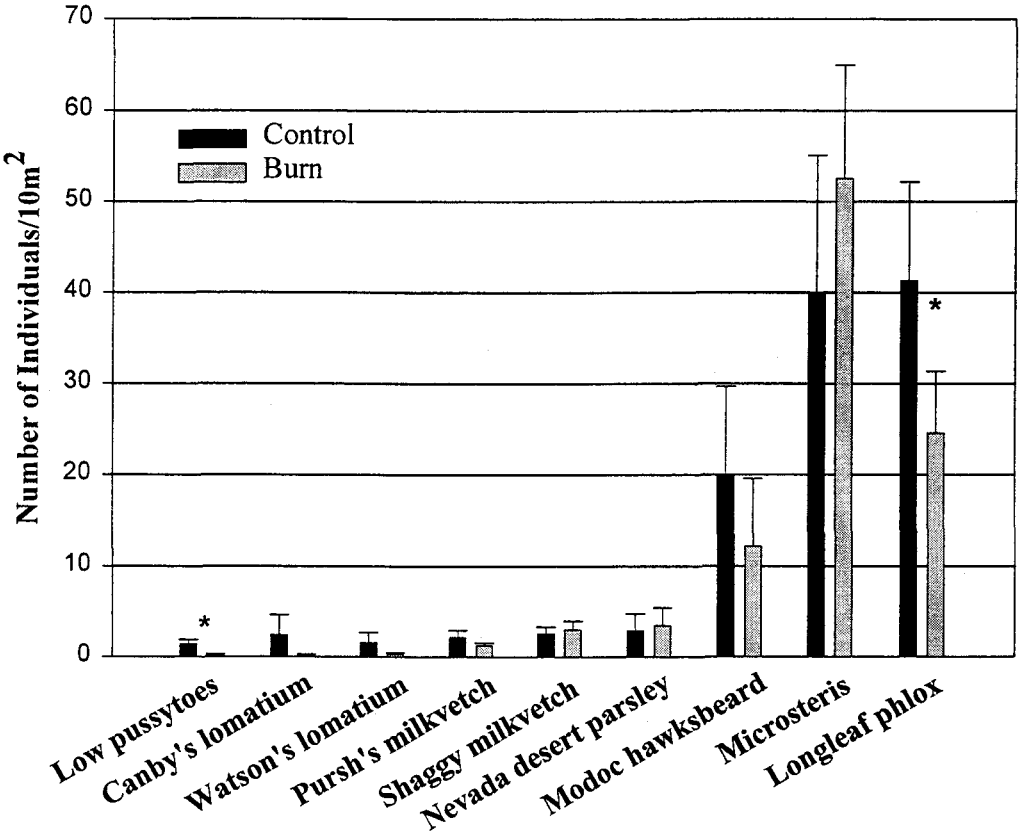

Figure 14. Density (individuals $10m^{-2}$) (+SE) of selected herbaceous dicot species in control and burn plots within the Wyoming big sagebrush ecosystem.

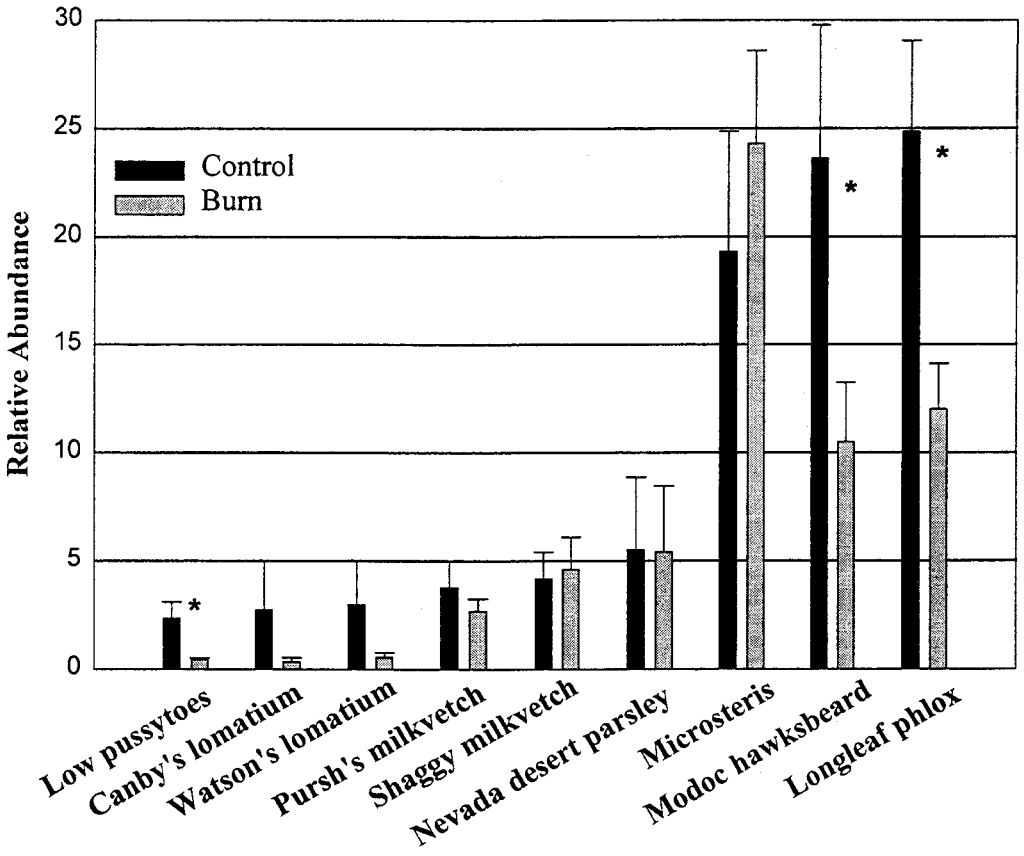

Figure 15. Relative abundance (+SE) of selected herbaceous dicot species in control and burn plots within the Wyoming big sagebrush ecosystem.

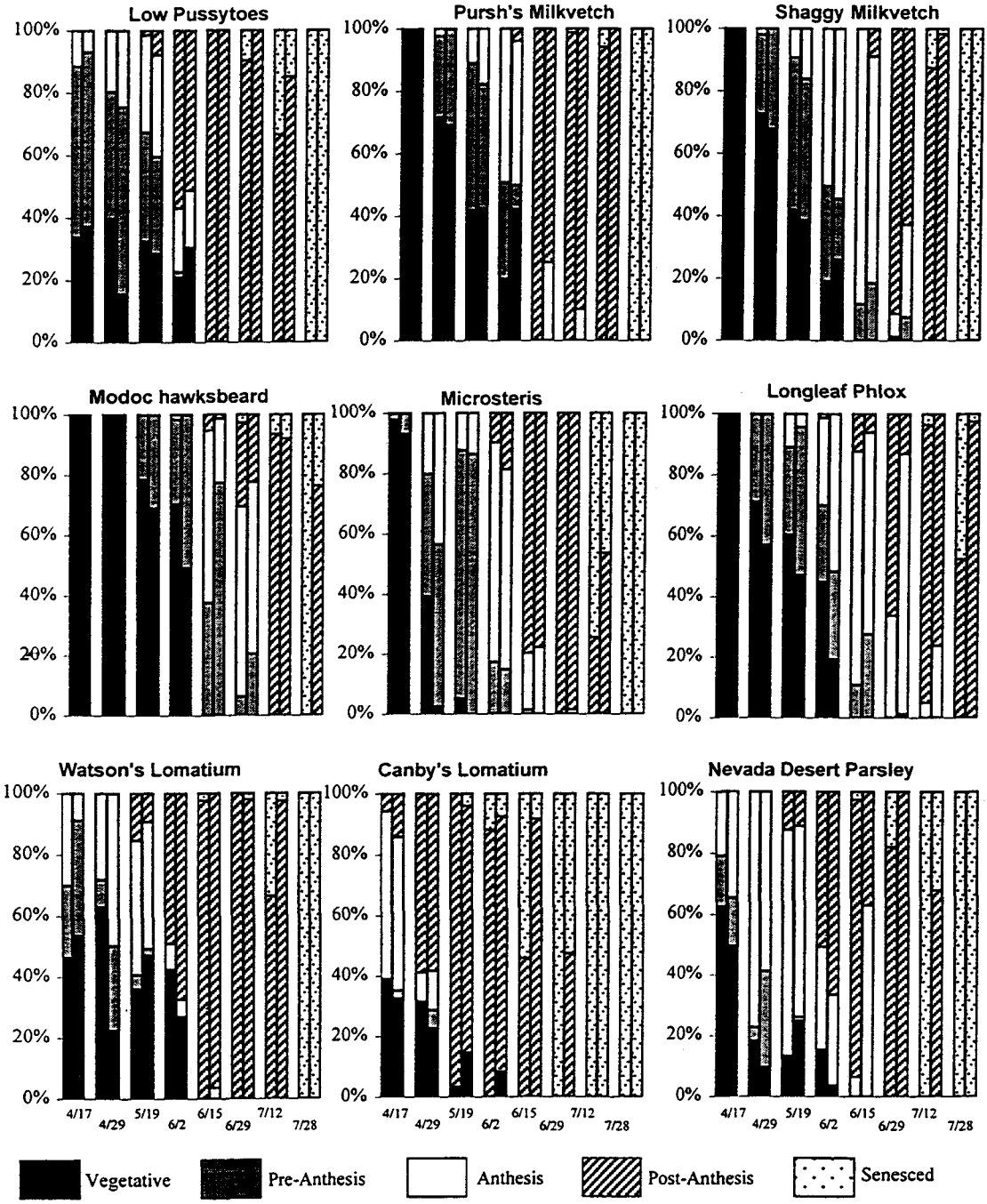

Figure 16. Percent of individual plants in various phenological stages within control (first bar at each date) and burn (second bar at each date) plots during the 1998 growing season in the Wyoming big sagebrush community.

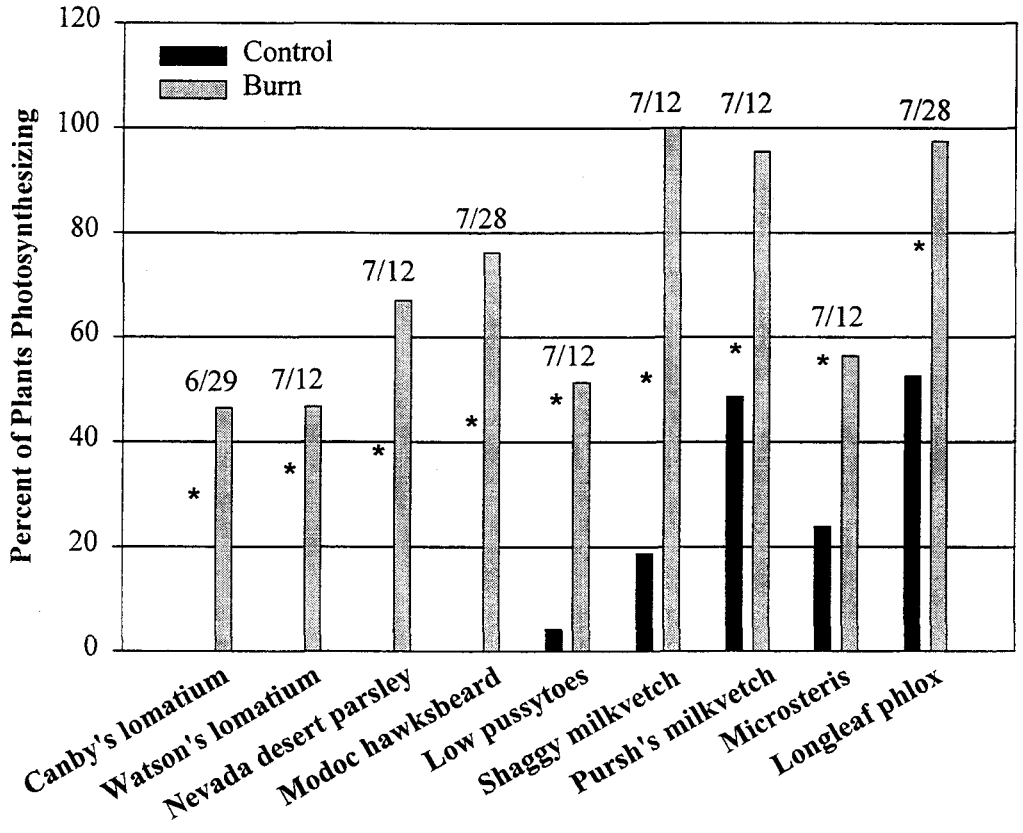

Figure 17. Percent of plants photosynthesizing in burned and control plots during the final sampling period of the summer for each species the Wyoming big sagebrush ecosystem. An * indicates significance at α=0.10.

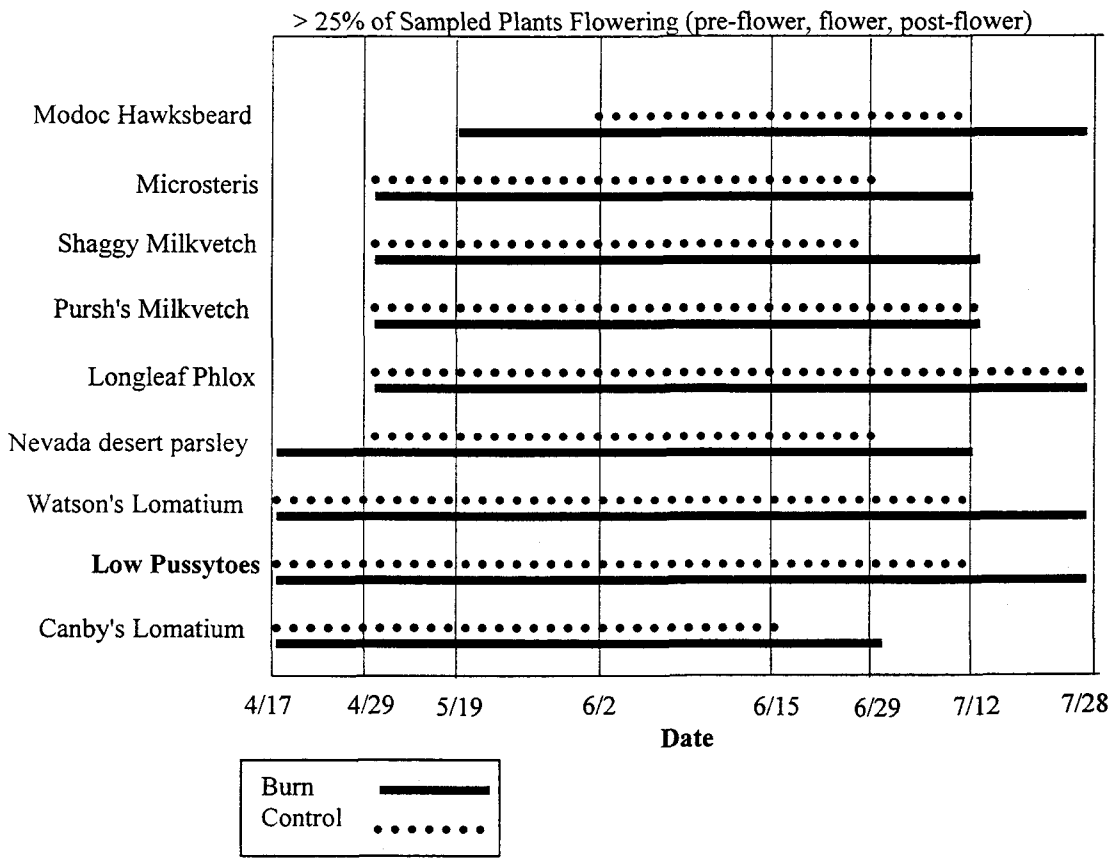

Figure 18. Period of time for which reproductive parts were available on a large proportion (>25%) of individuals of the selected species in the Wyoming big sagebrush ecosystem.

Table 5. Frequency, density, and relative abundance of dicot species prevalent in diets of sage grouse within the Wyoming big sagebrush study area.

	Frequency (mean % ± SE)				**Density** (mean # $10m^{-2}$ ± SE)				**Relative Abundance** (mean ± SE)			
Species	**Control**		**Burn**		**Control**		**Burn**		**Control**		**Burn**	
Shaggy milkvetch	12	3.9	14	4.2	3	0.8	3	0.9	4	1.2	5	1.5
Pursh's milkvetch	12	4.1	8	1.4	2	0.7	1	0.3	4	1.2	3	0.6
Canby's lomatium	5	3.7	1	0.4	2	2.2	0.2	0.1	3	2.3	0.3	0.2
Nevada desert parsley	11	6.5	12	7.0	3	1.9	3	2.0	6	3.3	6	3.1
Watson's lomatium	7	5.0	2	1.0	2	1.1	0.3	0.2	3	2.1	1	0.2
Microsteris	29	6.4	40	5.4	40	15.4	53	12.4	19	5.5	25	4.2
Longleaf phlox	41	5.8	24	4.5	38	9.1	25	6.8	24	4.0	12	2.1
Low pussytoes	8	1.8	1	0.3	1	0.4	0.2	0.1	2	0.7	0.4	0.1
Modoc hawksbeard	47	7.6	29	8.0	20	9.7	12	7.4	24	6.2	11	2.7
Ovalleaf buckwheat	19	0.9	3	1.1	5	0.7	0.5	0.2	8	0.5	0.9	0.3
Broom buckwheat	2	1.4	1	1.1	7	4.0	8	3.3	1	1.0	1	0.6
Mat buckwheat	0.9	0.5	0.1	0.1	0.2	0.1	0.02	0.02	0.2	0.1	0.01	0.01
Arcane Milkvetch	6	2.0	1.2	0.5	2	0.6	0.2	0.1	3	0.8	0.5	0.2
Donnell's lomatium	11	7.5	2	2.0	3	1.7	0.5	0.5	3	1.8	0.6	0.6
Nine-leaved desert parsley	0.1	0.1	0	0	0.01	0.01	0	0	0.01	0.01	0	0
Broadsheath lomatium	0	0	0.1	0.1	0.01	0.01	0.1	0.1	0.01	0.01	0.02	0.02
Tapertip hawksbeard	3	1.1	1	0.7	0.8	0.3	0.3	0.2	1	0.2	0.4	0.3
Mountain dandelion	1	0.6	0.5	0.2	0.6	0.4	0.2	0.1	0.5	0.4	0.2	0.1
False agoseris	0.1	0.1	0.2	0.2	0.01	0.01	0.1	0.1	0.1	0.1	0.1	0.1

Effects of Prescribed Fire on Abundance of Arthropods

Overall, ground-dwelling arthropod abundance (beetles, ants, and others) increased significantly in burned plots ($p=0.126$) (Figure 19). Prescribed fire treatment caused average ant abundance to increase from pre-burn levels by 116± 84 ants in treatment plots, and 6± 2 ants in control plots ($p=0.02$). Abundance of beetles and other arthropods were not affected by fire.

Table 6. Mean percent of individuals of selected dicot species which flowered in the prescribed burn and control plots during 1998. An "*" indicates that a significant difference existed at $\alpha=0.10$.

	Burn		Control	
Species	Mean	SE	Mean	SE
Low pussytoes	70	4.7	73	2.3
Shaggy milkvetch	67	3.3	68	6.7
Pursh's milkvetch	57	8.7	72	7.9
Modoc hawksbeard *	41	2.1	25	5.3
Canby's lomatium	89	3.5	94	3.4
Nevada desert parsley	86	4.0	88	1.6
Watson's lomatium	62	4.9	62	12.6
Longleaf phlox *	65	9.4	45	2.4

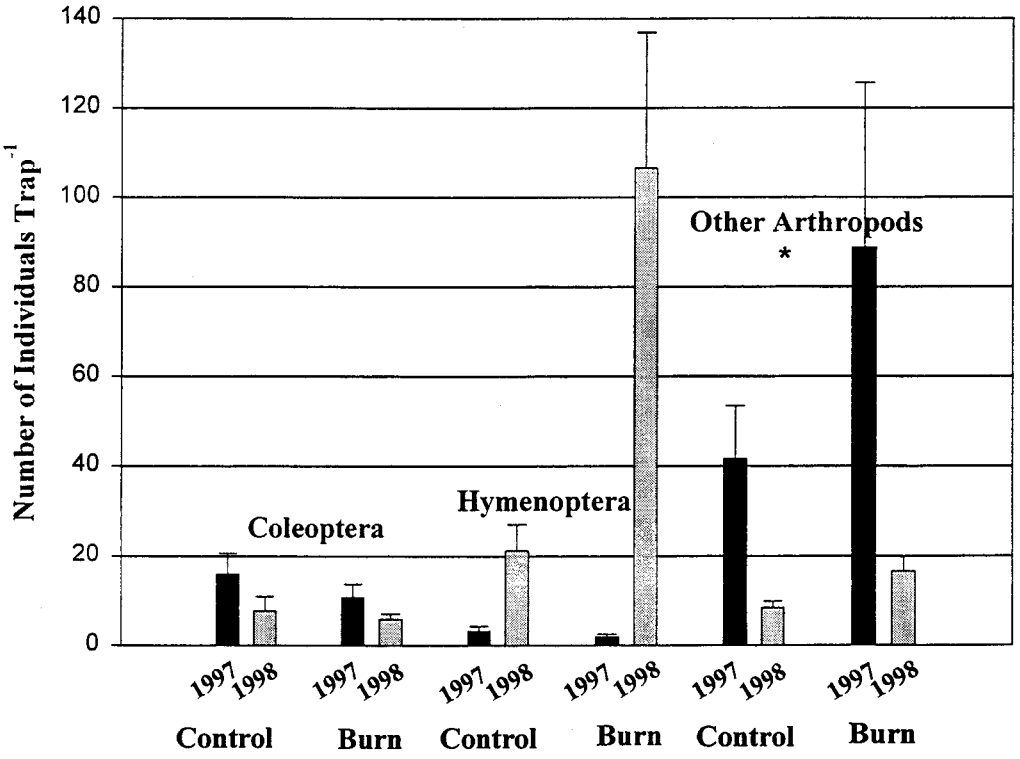

Figure 19. Mean number of coleoptera, hymenoptera, and other arthropods (+SE) in burned and control plots in the Wyoming big sagebrush ecosystem. An * indicates significance at α=0.10.

Discussion

Morphological Response to Fire

Reproductive effort by individual plants of at least 5 species was greater in first-year burned areas indicating that fire-enhanced flowering occurred in some of the herbaceous dicot species used by sage grouse. Increased flowering after fire has been observed in many species of grasses (Poaceae), other monocotyledons, but in few dicotyledons (Gill 1981, Sapsis 1990). Potential reasons for fire-enhanced flowering may be the increase in soil moisture, light, and available nutrients after fire (Kauffman et al. 1997). Old (1969) observed that nitrogen application (200lb/acre) also enhanced flowering of prairie grasses in Illinois.

The treatment difference in flowering was most profound in microsteris, which was the only annual plant studied. Annual plants have been observed to possess a greater ability to take advantage of the increased nitrogen availability (McLendon and Redente 1991) which occurrs after fire (Kauffman et al. 1997). This response, however, was not limited to annuals because increased flowering was also observed in perennials such as the *Lomatium spp.*, Modoc hawksbeard, shaggy milkvetch, and longleaf phlox. Fire-enhanced flowering has also been noted in Bradshaw's lomatium (*Lomatium bradshawii* (Rose ex Math.) Math. & Const) where frequent burning elevated numbers of umbels and seeds produced over unburned plants (Pendergrass et al. 1999). Other studies have found an increase in dicot cover two or more years post-fire (Sapsis 1990, Pyle and Crawford 1996), which could be a consequence of increased reproduction the first post-fire year.

Low pussytoes was the only species negatively affected by fire (reduced size and abundance). This reduction indicates that the species is not adapted to resist fire well and may survive by avoiding fire (e.g. avoider strategy of survival sensu Agee 1993) or by invading burned areas after fire. Low pussytoes posesses wind dispersed seeds (D. Wrobleski, pers. obs.) which should promote rapid dispersal. On our study area, this species often grows in rockier soils or rock crevices, which are areas where fire would not carry or be reduced in intensity thus reducing individual plant mortality.

Response of Dicot Abundance to Fire

Modoc hawksbeard, longleaf phlox, and low pussytoes were less abundant in burned plots. For Modoc hawksbeard this was likely due to the lower abundance prior to burning and not likely a fire effect. Reduced frequency of low pussytoes could be related to the positioning of its growth meristems above the soil surface where they may be damaged by high heat from fire (Daubenmire 1968). Modoc hawksbeard and low pussytoes have achenes which are wind dispersed. As a result, these species have the potential to re-establish or increase in abundance in burned areas within a few years after a fire. Longleaf phlox may have been reduced in frequency and relative abundance by fire because of its aboveground growth meristems. Fire-enhanced flowering in longleaf phlox and Modoc hawksbeard may facilitate increases in establishment on burned areas in subsequent years.

The positive influence of fire on flowering has been noted to have positive effects on seed production (Mark 1965, Pendergrass et al. 1999). This, coupled with the lack of negative effects on plant abundance (with the exception of low pussytoes and longleaf phlox) may increase abundance of many of these species in subsequent years. Areas of bare ground made available by fire could also serve as germination sites for seeds during initial post-fire years (Curtis et al. 1948).

Phenological Response to Fire

The longer period of active photosynthesis that I observed in all selected species in burned plots was likely a result of the higher soil moisture reported after fire (Kauffman et al. 1997). The extended flowering period in burned areas during the late summer was due to the later senescing, and thus longer period of non-dessicated seeds in the burned plots. It is likely that increases in soil temperature early in the growing season (Kauffman et al. 1997) caused the earlier availability of flowers in Modoc hawksbeard and Nevada desert parsley.

The greater proportion of Modoc hawksbeard and longleaf phlox individuals which flowered in burned plots during the first post-fire growing season may be caused by several factors. Differential fire survival of mature vs. immature plants may have resulted in a greater proportion of mature plants in burned areas. Differential fire survival may be related to increased root depths of older plants. Also, the increase in availability of nutrients, water, and solar radiation may have caused individuals in the burned plots to mature in only one year.

Fire Effects on Arthropod Abundance

Populations of arthropods appear to be able to maintain themselves through disturbance by fire. Fisher et al. (1996) found no increase in ants during the first post-fire year, and subsequent decreases during the second and third post-fire years. Similar to our study, Pyle and Crawford (1996) found no changes in abundance of beetles in relation to burning in a mountain big sagebrush/ bitterbrush (*Purshia tridentata* Pursh) community near our study area. The lack of changes in beetle abundance is thought to be due to adequate understory grass and forb habitat remaining after fire (Parmenter and MacMahon 1984).

Potential Effects on Sage Grouse Habitat

Fire-enhanced flowering in several of the dicot species measured in this study may improve forage availability for sage grouse during the pre-laying and brood-rearing periods. Greater numbers of inflorescences and flowers would provide pre-nesting female and young sage grouse with increased quantities of higher quality food. Abundance of 8 of the 9 important food species I studied was not affected one year after fire. Fire-enhanced flowering and germination areas opened by burning may facilitate reestablishment, and abundance of these species may increase through time.

By extending the period of potential photosynthesis and plant succulence on these herbaceous dicot species, forage quality will remain higher for sage grouse and other wildlife later into the dry season. The earlier flowering of Nevada desert parsley and Modoc hawksbeard increases the availability of high quality reproductive plant parts to sage grouse during the initial part of the growing season, when pre-laying females need nutrition the most. Rasmussen and Griner (1938) observed young sage grouse to forage on arthropods in relation to their availability, thus increases in ants will provide a benefit to sage grouse chicks. The first year following fire, the abundance of several dicot species was not affected, however fire has increased the reproductive effort and the length of time these species are available, in addition to increasing availability of ants. These changes in burned areas, juxtaposed with adjacent unburned areas to provide habitat for other needs, may have positive effects on sage grouse habitat.

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CHAPTER 4

CONCLUSION

Fire within this Wyoming big sagebrush ecosystem has removed the sagebrush from a portion of the area. Greater numbers of reproductive shoots in sagebrush along the edges of burned areas and the germination of sagebrush seedlings in burned areas will enhance sagebrush re-invasion into burned areas. Although structure was altered by removal of shrub dominance in the short-term, species composition has not been changed with the burned plots. During the first year after fire, plots were dominated by annual and resprouting herbaceous vegetation although all species were present. Fire did not significantly reduce the cover or frequency of perennial forbs, and increased the cover of annual forbs. Cover of perennial grasses was reduced by fire, but frequency and density of these species were unaffected by fire. The reduction in perennial grass cover is likely a short-term effect. No changes in annual grass cover or frequency were detected. Thirteen years post-fire, both the pulse in annual forb cover and reduction in perennial grass cover have returned to levels similar to unburned areas. No changes in alpha or gamma diversity were detected, however the combination of burned and unburned areas on the landscape increased species richness

Many of the herbaceous dicot species upon which sage grouse feed are positively affected by fire. Burning enhanced reproductive effort in 5 of 9 selected dicot species and did not negatively affect the others. Size of individual plants increased for 2 species, decreased in 1 species, while 6 others were unchanged. Burning reduced abundance of 2 species, while others remained unaffected. Prescribed fire also increased the proportion of individuals flowering in 2 species. Phenologically, all 9 species photosynthesized longer, and 2 species flowered sooner in burned areas.

Increases in annual forb cover, increases in plant size, and the extended growth and flowering period will enhance food availability for sage grouse spatially and temporally. Increases in flowering effort will increase food availability and may result in higher abundance of food species in the future. This should offset short-term reductions in abundance some species. Higher food availability for pre-laying sage grouse females and chicks may have positive effects on sage grouse nutrition. Reductions in cover of sagebrush and other shrubs will reduce nesting and wintering habitat in the short term. Greater numbers of sagebrush shoots along burn edges and existing seedlings will enhance sagebrush re-invasion to restore nesting habitat. The positive response of sagebrush along burn edges may even enhance nesting habitat quality along edges. The high amounts of sagebrush remaining at the landscape level, high interspersion of burned and unburned patches, and positive effects of fire within burned patches may have positive effects on sage grouse habitat.

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