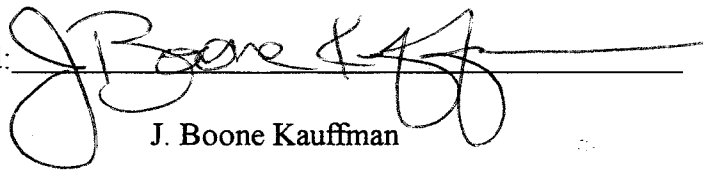AN ABSTRACT OF THE THESIS OF

_Douglas William Havlina_ for the degree of _Master of Science_ in

_Rangeland Resources_ presented on _January 27, 1995_.

Title: _Fire Effects on Vegetation Diversity, Structure, and Successional Dynamics in Shrub-Steppe and Mixed Conifer Environments of the Hells Canyon, Idaho._

Abstract approved:

J. Boone Kauffman

The effects of fire severity on post-fire succession and shrub demography were quantified in shrub-steppe grasslands and subalpine forests in the Hells Canyon of the Payette National Forest, Idaho. Following the 1988 Eagle Bar Fire, species frequency, community diversity, fire adaptations, and stand ages were quantified at 12 plots in burned and unburned forests. Pre-fire composition was dominated by _Pseudotsuga menziesii_, _Pinus contorta_, _Abies grandis_, and _Abies lasiocarpa_ in the overstory. Pre-fire basal area ranged from 41 to 80 $m^2$ $ha^{-1}$. Pre-fire stand ages ranged from 71 years in _Abies lasiocarpa_ forests to > 200 years in _Pseudotsuga menziesii_ stands. Fire scenarios which were sampled consisted of: (1) complete stand-replacement fires; (2) partial stand-replacement fires; and (3) unburned forests (control). Partial stand-replacement forests were characterized by significantly higher mean species diversity and richness (H'=3.16, S=36) than complete stand-replacement (H'=2.78, S=27) or unburned forests (H'=2.26,

S=15). Vegetation preferentially established in burned areas along a gradient of fire severity according to adapted fire guilds. Single-storied forests dominated by *Pinus contorta* and *Abies lasiocarpa* typified stand-replacement fire scenarios, with mean ages ranging from 99 to 159 years corresponding to fire return intervals common in this type. Multi-storied forests of *Pseudotsuga menziesii* in the overstory and *Abies* spp. in the mid-story comprised partial stand-replacement forests. Overstory stand ages ranged from 165 to 209 years, while mid-story ages ranged from 77 to 99 years, corresponding to fire-return intervals which characterize the intermediate, partial stand-replacement fire regime. In the Hells Canyon forests, fire is a dominant ecosystem process in the creation of landscape mosaics, in governing species distribution, and in the maintenance of biological diversity.

Forests experiencing complete stand-replacement (n=4) were dominated by *Salix scouleriana*, a classic off-site colonizer. At the fourth post-fire year, *Salix scouleriana* density ranged from 252,000 shrubs ha$^{-1}$ to 569,333 shrubs ha$^{-1}$. From the fourth to the fifth post-fire year, mean shrub density showed a significant decrease from 336,667 to 246,000 shrubs ha$^{-1}$. During this same period, mean shrub biomass significantly increased from 10.2 g shrub$^{-1}$ to 33.1 g shrub$^{-1}$, mean aboveground biomass significantly increased from 2.95 to 7.05 Mg ha$^{-1}$, and mean shrub height significantly increased from 62 to 100 cm shrub$^{-1}$. Without competing conifers, *Salix scouleriana* may maintain site dominance for several decades.

The 1992 Windy Ridge Fire burned approximately 2,000 ha of the *Purshia tridentata/Agropyron spicatum* plant association at elevations < 1460 m. Because *Purshia tridentata* survivorship appeared to be associated with plant age and ecotype, a

multiple regression model was developed to partition burned and unburned shrubs into age class segments at n=10 sites. Pre-fire shrub density ranged from 400 to 1700 shrubs ha$^{-1}$. Concomitant with *Purshia tridentata* decadence and stagnation following a lengthened fire-free interval were increases in post-fire mortality. Post-fire mortality of *Purshia tridentata* was closely associated with plant age ($R^2$=0.91). Plants in age classes < 25 years of age exhibited 66% sprouting, while shrubs > 25 years of age had only 20% survival. Shrub mortality in burned communities ranged from 37% to 100%, while mortality among unburned communities averaged 5%. The reintroduction of fire appears to be a necessity for restoring certain *Purshia tridentata* ecotypes which have not entered stagnation. Continued fire exclusion may well result in the loss of many at risk *Purshia tridentata* communities.

As an influence on ecosystem function, genetic variation, and landscape mosaics, fire represents a pervasive disturbance in the Hells Canyon ecosystems. Unique successional pathways result from fires which vary in dimension, severity, and periodicity, thereby contributing to diversity at all scales. Intrinsic adaptations to fire testify to the coevolution between flora and fire in the Hells Canyon, and illustrate the resiliency of biota in fire-dominated environments.

FIRE EFFECTS ON VEGETATION DIVERSITY, STRUCTURE, AND
SUCCESSIONAL DYNAMICS IN SHRUB-STEPPE AND MIXED
CONIFER ENVIRONMENTS OF THE HELLS CANYON, IDAHO

by

Douglas William Havlina

A THESIS

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in partial fulfillment of
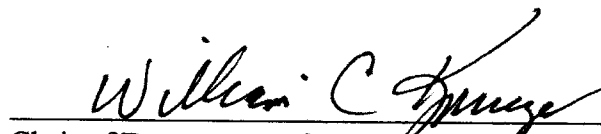the requirements for the
degree of

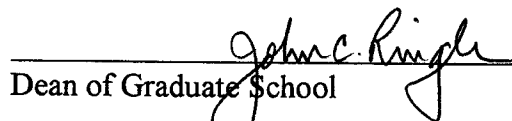Master of Science

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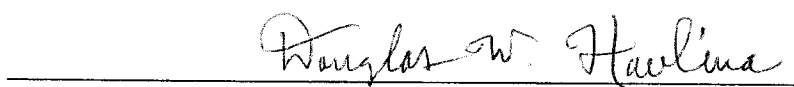
APPROVED:

Major Professor, representing Rangeland Resources

Chair of Department of Rangeland Resources

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.

Douglas William Havlina, Author

# DEDICATION

The efforts of this thesis are dedicated with love to the memories of my grandparents, Chet and Pearl Havlina, Tulelake settlers.

# ACKNOWLEDGEMENTS

Thanks to you, Heather C. Miller, for the night at the hospital, enduring hours of computer torture, listening to all my songs, and your many positive contributions to the editing and construction of my thesis. I must owe you "many big gifts" for all your help?!

Thanks to Carolyn Aslett for your love through the years, and to Jim Aslett for challenging me to follow my dreams. My gratitude to Joe and Bob for memories past and yet to come, and for your friendship.

Finally, my thanks to everyone who in some way has influenced my thinking and challenged me to explore my limits. As I close this chapter in time, I hope my future dreams will follow the words of *Four Quartets*, where T.S. Eliot challenges humanity to grow in vision, passion, and in so doing, in understanding:

> Old men ought to be explorers...
> For a further union, a deeper communion
> Through the dark cold and the empty desolation,
> In my end is my beginning.
>
> --T.S. Eliot, *Four Quartets*

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# FIRE EFFECTS ON VEGETATION DIVERSITY, STRUCTURE, AND SUCCESSIONAL DYNAMICS IN SHRUB-STEPPE AND MIXED CONIFER ENVIRONMENTS OF THE HELLS CANYON, IDAHO

## CHAPTER I
## INTRODUCTION

As the deepest gorge in the continental United States, the Hells Canyon separating Idaho and Oregon contains a wealth of ecological resources. Grassland and forest communities support diverse assemblages of flora and fauna which contribute to the many values associated with the area. Primitive recreation, livestock grazing, and timber harvest are uses which have continued since Euro-American homesteading in the 1870s (USDA Forest Service, Hells Canyon NRA Environmental Impact Statement 1979).

The vegetation composition within the Hells Canyon is highly diverse, due in part to elevations ranging from 244 m at the Snake River to 2865 m at the summit of He-Devil mountain. Grasslands occupy a band at elevations < 1200 m, while an ecotone encompassing grass, shrub, and scattered conifer types exists between approximately 1200 m and 1600 m. Forests dominated by *Pinus ponderosa* Dougl., *Abies grandis* [Dougl.] Forbes, and *Pseudotsuga menziesii* [Mirbel] Franco occur between 1600 m and 1900 m. At elevations > 1900 m, subalpine forests dominated by *Pinus contorta* Dougl., *Pseudotsuga menziesii*, *Abies lasiocarpa* [Hook.] Nutt., and *Abies grandis* are interspersed with alpine meadows (This Study, USDA Forest Service Hells Canyon NRA Environmental Impact Statement 1979).

The unique recreational, aesthetic, and ecological values of the Hells Canyon ecosystems were recognized in 1975 with the creation of the Hells Canyon National Recreation Area, encompassing 264,258 ha of wilderness and semi-primitive lands. These ecosystems represented communities valued for wildlife habitat, fisheries, and primitive recreation opportunities under multiple-use management. More recently, the USDA Forest Service has adopted Ecosystem Management as a holistic concept to manage for ecological outcomes rather than commodity outputs. Ecosystem Management incorporates management activities (e.g., timber harvest, prescribed fire, livestock grazing) as tools to achieve a predetermined landscape structure, function, and composition (i.e., a desired future condition). Management which replicates or provides for the continuation of ecological processes is a pivotal theme of Ecosystem Management.

A cornerstone of Ecosystem Management is the description of desired future conditions (DFC). The DFC is necessarily fire-related, because wildfires are a prevalent historic disturbance in the Hells Canyon, as they are for most other terrestrial North American ecosystems (Agee 1993, Johnson and Simon 1987, Tisdale 1986). Inherent in determining desired future conditions are considerations of biological diversity and structural complexity at the community, landscape, and regional scales.

In historical and contemporary forests of the Hells Canyon, fire has been and continues to be a prominent disturbance process in shaping landscape structure and biological diversity. Low severity fires recurring every 2 to 20 years maintained low shrub densities and promoted grasslands in the Hells Canyon (Crane and Fischer 1986).

In contrast, the higher elevation subalpine forests are characterized by infrequent, variable severity fire events occurring on the order of every 100 to > 300 years (Agee 1993, Crane and Fischer 1986). Fire events between shrub-steppe and subalpine environments represent the extremes in fire regimes and effects on long-term succession. Even within similar environments, variable fire severities influence biodiversity through initiation of multiple pathways of succession. However, the relationship between fire events, fire survival adaptations, successional sequences, and specific desired future conditions are poorly understood in ecosystems of the Hells Canyon.

Crane and Fischer (1986) concluded that highly variable, multiple pathways of succession typify forest communities of west-central Idaho. Agee (1993) suggested that the management of natural resources is best achieved following an understanding of historic disturbance processes, including fire. Lotan et al. (1981) stated that including fire as a component of holistic management requires an ability to interpret ecological responses to fire in the context of the historic fire regime. To best describe desired future conditions in these ecosystems, site-specific information along gradients of seral development is needed. Continued research addressing disturbance ecology in the environments of the Hells Canyon is central to ecosystem-based decision making.

The central hypothesis of this research was that variation in the timing and severity of fires would result in the establishment of distinct seral associations, with differential effects on shrub demography and survivorship, biological diversity, successional sequences, and structural complexity.

To test this hypothesis, post-fire succession was quantified following two fire events in the Hells Canyon of west-central Idaho. Twelve experimental plots were established following the 1988 Eagle Bar Fire. Four replicates of each of the following forest scenarios were examined: (1) forests experiencing complete stand-replacement (complete overstory mortality); (2) forests experiencing partial stand-replacement (partial overstory mortality); and (3) forests which were unburned (control). Comparisons of differences in species composition, richness, and diversity were made. In addition, dynamics of the dominant *Salix scouleriana* populations during the fourth and fifth post-fire years in forests experiencing stand-replacement fire were quantified. Ten experimental plots were established following the 1992 Windy Ridge Fire in shrub-steppe communities to quantify variables influencing the survivorship of *Purshia tridentata*.

The primary research goal is to provide resource managers with site-specific information on the role of fire in several Hells Canyon ecosystems. It is hoped that findings presented herein regarding biological diversity, fire severity, and successional pathways will contribute to a greater understanding and the appropriate use of fire in ecosystem-based management.

This thesis has been arranged into five chapters to simplify organization. The following chapter addresses the effects of fire severity on community diversity, forest structure, and successional pathways, and describes fire guilds which facilitate survival in fire-dominated subalpine forest ecosystems. Chapter three includes details of the autecology of *Salix scouleriana* as affected by fire severity, and dynamics of shrub

biomass, height, and density in the fourth and fifth post-fire years. Chapter four

examines the age class distribution of *Purshia tridentata* communities, fire survivorship,

and historic fire-return intervals, and explores the regional dilemma of *Purshia tridentata*

in the Great Basin and Pacific Northwest. Chapter five is a summary of the major

themes of each chapter.

# CHAPTER II
## FIRE EFFECTS AND COMMUNITY DIVERSITY IN
## SUBALPINE FORESTS OF THE HELLS CANYON, IDAHO

## Abstract

Among subalpine forests, a reciprocal suite of relationships exist between vegetation composition, structure, and fire severity. The effect of two levels of fire severity on plant community composition and structure was quantified in subalpine forests of the Hells Canyon, Idaho. Prior to fire, forests were dominated by even-aged stands of *Pinus contorta*, *Abies lasiocarpa*, and *Abies grandis*, or multi-aged stands of *Pseudotsuga menziesii* and *Abies lasiocarpa*. Species composition, richness, diversity, evenness, and pre-fire stand age were quantified in unburned forests, and those following partial stand-replacement and complete stand-replacement fires associated with the 1988 Eagle Bar Fire. The partial stand-replacement fires which were of moderate fire severity had significantly greater species richness, species evenness, and species diversity than either unburned or the complete stand-replacement fires. In contrast, unburned forests exhibited the lowest species richness, species evenness, and species diversity. Species diversity (H', Shannon Diversity Index) ranged from 1.91 in unburned forests to 3.36 in partially burned forests. These findings support the "intermediate disturbance hypothesis", stating that the highest diversity exists in environments experiencing disturbance of moderate severity and frequency. Pre-fire stand age and forest structure were found to correlate closely with two distinct fire regimes.

There was a linkage between forest structure and fire which exemplified the circular relationship between the biotic structure and fire severity. The high severity stand-replacement fires occurred in even-aged forests dominated by *Pinus contorta* and *Abies lasiocarpa*. These forest stands were typified by infrequent (100-300 year), high severity fire events. In contrast, the partial stand-replacement fires occurred in uneven-aged forests of *Pseudotsuga menziesii* and *Abies lasiocarpa*. In these stands, the fire regime could be considered variable with frequent (50-100 year), moderate severity fire events superimposed by infrequent (100->200 year), stand-replacing fire events.

A suite of ecological adaptations was directly linked to post-fire successional pathways and species composition. Post-fire dominants in the stand-replacement forests (e.g., *Salix scouleriana*, *Epilobium* spp.) largely established from mobile, wind-borne seed sources (invaders) or from long-lived seed sources stored in the soil or canopy (evaders). In contrast, dominants in the partial stand-replacement forests (e.g., *Thalictrum occidentalis*, *Valeriana sitchensis*) typically survived the fire by sprouting from root crowns, taproots, or other subterranean organs (endurers). Forests experiencing complete stand-replacement were characterized by a higher proportion of evaders and invaders, while endurers comprised a higher proportion of the post-fire community in partial stand-replacement fires. Unburned forests exhibited the greatest proportion of avoiders--species existing in late seral conditions having few fire survival mechanisms.

# Introduction

In the Hells Canyon of Idaho and Oregon, fire has been a pervasive ecosystem disturbance process that has influenced the spatial and temporal distribution of endemic flora (Johnson and Simon 1987). Fires from anthropogenic and natural sources served to shape both landscape structure and biological diversity, and reinitiate successional sequences (Crane and Fischer 1986). Because of variability in the fire environment (e.g., fuels, topography, aspect, forest composition, forest structure), heterogeneity in the size, frequency, and severity of burning is typical for fires in this ecosystem (Martin and Sapsis 1991). Resulting post-fire "mosaics" are characterized by structural discontinuities at the landscape, community, and population scales (Sousa 1984).

Biological diversity is defined as the aggregate and distribution of life and ecological processes that influence the biota in a given area (Magurran 1988). Inclusive in biological diversity is diversity at the landscape, community, and population scales, of which fires have a dramatic effect. Species richness (the absolute number of species) and species abundance (the distribution of species) are the most often used descriptors of biological diversity at the community level (Ludwig and Rehnolds 1988).

Variation in fire severity and periodicity, termed "pyrodiversity" (Martin and Sapsis 1991), is a dominant contributor to biodiversity at all scales. In the Hells Canyon of Idaho, recent fire events (Deep Creek Fire, 1994; Hells Canyon Complex, 1989; Eagle Bar Fire, 1988; Echels Creek Fire, 1960) clearly indicate that fire is a prevalent disturbance factor in this ecosystem. Community diversity may be enhanced by fires

which create niches for a high number of species (Connell and Slatyer 1977). Fire may enhance ecosystem diversity through altering patch sizes, edge amounts, and connectivity of communities (Spies 1992). At a landscape scale, biodiversity can be influenced from the mosaics of varied age classes, species compositions, and successional pathways following fire. At the regional scale and at temporal scales of centuries, fire events influence biodiversity at all levels.

Measures of species diversity have recently been utilized as indicators of ecosystem resilience and stability (Magurran 1988). Considering the dramatic disturbance role that wildfire has played, and continues to play in shaping the structure and function of the Hells Canyon ecosystems, quantifying the relationships between fire severity, biological diversity, and successional development is important. To better understand these relationships, the following study objectives within the perimeter of the Eagle Bar Fire were established: (1) describe relationships between fire regimes for subalpine forests, and the associated stand age class structure; (2) quantify species composition and diversity in forest stands following partial stand-replacement fires, complete stand-replacement fires, and unburned forests; and (3) to describe plant adaptations facilitating species survival and persistence following wildfire in the Hells Canyon, Idaho.

## Study Area

The study area was located within the perimeter of the Eagle Bar Fire, on the Payette National Forest, Idaho. The Eagle Bar Fire began at midday on 21 August, 1988 along the Snake River. The fire initially burned in low elevation grasslands, but progressed to the higher elevation forested communities at the rim of the Hells Canyon. The fire ended by 2 September after encountering sparse fuels and cooler temperatures at the canyon rim (> 2140 m). The Eagle Bar Fire burned approximately 7096 ha, including 3200 ha of subalpine forests dominated by *Abies lasiocarpa* [Hook.] Nutt., *Abies grandis* [Dougl.] Forbes, *Pseudotsuga menziesii* [Mirbel] Franco, and *Pinus contorta* Dougl. The study was conducted within these subalpine forests.

Field work was conducted from June through September, 1992-93. Three fire scenarios were intensively sampled: (1) severe, stand-replacement (SR) forests resulting from complete overstory mortality; (2) partial stand-replacement (PSR) forests experiencing partial fire-induced overstory mortality; and (3) unburned (UB) areas within the fire perimeter. Species composition and forest structure were quantified in 4 stands of each of these disturbance scenarios (i.e., n=12).

Criteria for site selection was based upon similarity among pre-fire species composition, slope, aspect, soils, and elevation. Sites were selected following field reconnaissance of the fire area. All sites selected were > 1700 m elevation, on northwesterly aspects, and had deep sandy loam skeletal soils (Table II.1.). The study area receives between 63 and 119 cm of precipitation annually. Precipitation averages

102 cm annually, with > 70% occurring as snow between November and March. The study area is characterized by short warm summers, and long, cold winters. The mean July temperature averages 12.2°C, the mean January temperature averages -10.0°C, and the mean annual temperature is 7.5°C (Larson et al. 1982, USDA Hells Canyon NRA Environmental Impact Statement 1979).

## Methods

## Composition and Diversity Measurements

Within each stand a 25 x 25 m plot was established based upon uniformity in fire effects. Severe, stand-replacement plots were selected based upon similarity in scorch height, overstory mortality, and topographic variables. Partial stand-replacement forests were selected based upon similarity in forest structure and species composition. Unburned forests were selected based upon similarity to the pre-fire structure of the severe and partial stand-replacement sites. Within each plot, five transects were established 5 m apart, parallel to the slope. Along each transect, six randomly located 50 cm x 50 cm microplots were established. Thus, a total 30 microplots were read each year within each replicate. Within each microplot, species presence was recorded for analysis of frequency. Species frequency for each site was calculated as the % of occurrence within all sampled microplots (i.e., a species occurring in 20 of 30 microplots would have 66% frequency).

## Fire Guild Assignment

Within the study area, all plants which were detected were assigned one or more fire guilds based upon their adapted strategies to survive fire events. Fire guilds were defined as the ecological traits facilitating species persistence or individual survival within a given fire regime. The fire guilds which were assigned were evaders, endurers, avoiders, resisters, and invaders, and are described in the discussion section (after Agee 1993).

## Overstory Structure and Age

Stand age at each replicate was quantified. In complete stand-replacement fires which were dominated by *Pinus contorta* and *Abies lasiocarpa*, trees were randomly selected outside of the plot for aging. In the uneven-aged communities (partial stand-replacement forests) which were dominated by *Pseudotsuga menziesii* and a mid-story of *Abies lasiocarpa* and *Abies grandis*, ages were quantified for both the dominant and suppressed strata. The species, status (live or dead), and diameter at 1.3 m (dbh) of all trees in the plot were recorded to quantify pre-fire basal area, stand density, and the dominant pre-fire conifers (Table II.1). In the severe stand-replacement fire scenarios where all trees were killed, stand age was quantified by cross sectional analysis of felled snags (n=80). In the partial stand replacement and unburned communities, n=5 living trees were bored with an increment borer to ascertain tree age.

## **Statistical Analysis**

Community analysis of species diversity and species evenness followed that of

Magurran (1988). The Shannon diversity index was selected because both diversity and

evenness values can be calculated from the formula, and it is reflective of species

richness (Magurran 1988, Ludwig and Rehnolds 1988). Species richness (S) was the

total number of species encountered in sampling. Species diversity was calculated by

summing the frequency of all species, and dividing the individual plant frequency by the

sum of the community frequency to arrive at a proportional abundance, $p_i$, for the $i$th

species ($n_i/N$). The formula for calculating the Shannon Diversity Index is:

$$H' = - \Sigma \, p_i \, lnp_i$$

Species diversity (H') and species richness (S) were used to calculate species

evenness (J'), using the formula:

$$J' = H' / ln \, S$$

A Student's t-test was used to test for significant differences between communities

($p < 0.01$), after calculating a diversity variance, after Hutcheson (1970). The test for

significant differences utilized the formula:

$$t = \frac{H'_1 - H'_2}{(Var \, H'_1 + Var \, H'_2)^{1/2}}$$

where $H'_1$ is the diversity for community 1, and $H'_2$ is the diversity for community 2, and

$Var \, H'_1$ and $Var \, H'_2$ are the respective variances.

## Results

### Species Frequency and Composition

Table II.2. is arranged to illustrate the gradient in species occurrence noted between the fire scenarios. Species frequency is listed in a gradient from complete stand-replacement to unburned forests. Plants were listed in the following order: those which were only detected in stand-replacement forests; plants which were in both stand-replacement and partial-stand replacement forests; plants detected only in partial stand-replacement forests; plants which were in partial stand-replacement and unburned forests; plants detected only in unburned forests; and, plants which occurred in stand-replacement, partial stand-replacement, and unburned forests.

The total number of species detected during sampling was 106. Thirty plant species (28%) occurred in all forest scenarios. The remaining species preferentially established on sites according to the disturbance severity. Fourteen species (13%) colonized exclusively on stand-replacement sites, while 15 species (14%) were found only in partial stand-replacement forests. Eleven species (10%) were detected only in unburned forests. Thirty-one species (29%) were common between stand-replacement and partial stand-replacement forests, and 5 species (5%) were common between partial stand-replacement and unburned forests. In forests experiencing stand-replacement, the 10 most frequent species, listed in order of occurrence, were: *Salix scouleriana* Barratt, *Epilobium angustifolium* L., *Anemone piperi* Britt., *Lathyrus*

Table II.1. Summary of study sites and pre-fire forest structure at the Eagle Bar Fire in the Hells Canyon, Idaho. Payette National Forest. UB=Unburned Plot, SR=Stand Replacement Plot, PSR=Partial Stand Replacement Plot. Standard errors are presented in parentheses for the mean of each treatment.

| | Dominant Pre-fire Conifer | Mean Basal Area (m² ha⁻¹) | Stems ha⁻¹ | Mean Diam. (cm) | Mean Pre-Fire Age (Years) of Dominant | Elev. (m) | General Aspect | Slope (%) | Legal Location |
|---|---|---|---|---|---|---|---|---|---|
| **Horse Mtn. South UB:** | *Abgr Abla* | 60.52 | 1968 | 17 | 73 | 1922 | NW | 56 | T 21N, R3W, Sec 24, SW/SW |
| **Horse Mtn. North UB:** | *Abgr Abla* | 53.05 | 1840 | 16 | 71 | 1976 | NW | 57 | T21N, R3W, Sec 24, NW/SW |
| **Saw pit South UB:** | *Psme* | 59.40 | 592 | 29 | 125 | 1998 | W | 41 | T21N, R3W, sec 2, SE/SW |
| **Saw pit North UB:** | *Psme* | 79.59 | 528 | 34 | 123 | 1970 | W | 46 | T21N, R3W, sec 2, NE/SW |
| **Unburned Mean:** | NA | 63.14 (8.23) | 1232 (672) | 24 (8) | 98 (26) | 1967 (22) | NA | 50 | NA |
| **Tussel Ridge PSR West:** | *Psme Abla* | 40.78 | 1392 | 16 | 188 | 1885 | NW | 49 | T21N, R3W, sec 14, SW/N |
| **Tussel Ridge PSR East:** | *Psme Abla* | 71.73 | 1168 | 21 | 201 | 2028 | NW | 56 | T21N, R3W, sec 14, SE/NE |

Table II.1., Continued

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **K. Point PSR:** | *Psme Abla* | 46.45 | 720 | 23 | 184 | 1976 | NW | 46 | T21N, R3W, sec 11 NW/SE |
| **Sheep Rock PSR:** | *Psme, Laoc* | 58.81 | 1296 | 20 | 172 | 1934 | N | 44 | T21N, R3W, sec 2, NE/NW |
| **PSR Mean:** | NA | 54.44 (10.83) | 1144 (212) | 20 (2) | 186 (8) | 1956 (46) | NA | 49 | NA |
| **Tussel Ridge SR West:** | *Psme Abgr* | 68.20 | 992 | 19 | NA | 1678 | NW | 46 | T21N, R3W, sec 14, SW/NW |
| **Tussel Ridge SR East:** | *Psme Abla* | 58.30 | 256 | 47 | 112 | 1804 | NW | 59 | T21N, R3W, sec 14, SE/NW |
| **Grassy Ridge SR:** | *Pico Abla* | 62.40 | 896 | 25 | 112 | 2036 | NW | 22 | T21N, R3W, sec 11, NW/SE |
| **Sheep Rock SR:** | *Pico Abla* | 45.50 | 832 | 24 | 132 | 1939 | N | 25 | T21N, R3W, sec 2, NW/NE |
| **SR Mean:** | NA | 58.60 (6.70) | 744 (244) | 29 (9) | 119 (9) | 1864 (123) | NA | 38 | NA |

*nevadensis* Wats., *Carex geyeri* Boott, *Viola canadensis* L., *Polygonum douglasii*

Greene, *Epilobium minutum* Lindl., *Bromus vulgaris* (Hook.) Shear, and *Pinus*

*contorta*. Of the fourteen species which occurred exclusively in stand-replacement

forests, 4 were from the Rosaceae family (*Physocarpus malvaceous* (Greene) Kuntze,

*Rosa gymnocarpa, Sorbus scopulina* Greene, *Spirea pyrimidata* Greene), 2 were from

the Fabaceae family (*Lathyrus nevadensis, Vicia americana* Muhl.), and 2 were from the

Asteraceae family (*Crepis acuminata* Nutt., *Taraxacum officinale* Weber). The plants

within these families had different specific adaptations to fire; the Rosaceous shrubs

exhibited basal sprouting, plants from the Fabaceae family established from a refractory

seed pool, and plants from the Asteraceae family exhibited the adaptation of colonization

through windborne seed.

Thirty-two species occurred in both stand-replacement and partial stand-

replacement forests. These were often species recognized as being highly adapted to fire

events, most notably *Salix scouleriana, Epilobium angustifolium, Epilobium*

*paniculatum* Nutt., *Epilobium minutum, Ceanothus velutinus* Dougl., and *Pinus*

*contorta* (Stickney 1986). Among each of these species, there was a significant decrease

in the frequency of occurrence from stand-replacement forests to partial stand-

replacement forests. This indicates that although they were also found in partial-stand

replacement forests, they are better suited to colonizing after severe, stand-

replacement fires.

In partial stand-replacement fire scenarios, the 10 most frequent species, listed in

order of occurrence, were: *Polemonium pulcherrimum* Hook., *Viola canadensis,*

Table II.2. Mean frequency (%) of species encountered in stand replacement, partial stand replacement, and unburned forests in the fourth and fifth post-fire years following the 1988 Eagle Bar Fire in the Hells Canyon, Idaho. (Citations: (1) This study, (2) Stickney 1986, (3) Fischer and Crane 1986, (4) Kauffman 1990).

| SPECIES | FIRE GUILD, LITERATURE CITATION | SR 92 | SR 93 | PSR 92 | PSR 93 | UB 92 | UB 93 |
|---------|--------------------------------|-------|-------|--------|--------|-------|-------|
| *Physocarpus malvaceus* | Endurer (Basal Sprouting): 1,3 | 3 | 0.75 | 0 | 0 | 0 | 0 |
| *Pinus contorta* | Evader (Semi-Serotinous Cones): 1,2 | 16 | 18 | 0 | 0 | 0 | 0 |
| *Rosa gymnocarpa* | Endurer (Basal Sprouting): 1,2 | 3 | 4 | 0 | 0 | 0 | 0 |
| *Sorbus scopulina* | Endurer (Basal Sprouting): 1,2 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Spirea pyramidata* | Endurer (Rhizomes): 1 | 0 | 3 | 0 | 0 | 0 | 0 |
| *Clarkia pulchella* | Invader (Wind Borne Seed): 1 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Crepis acuminata* | Invader (Wind Borne Seed): 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Lathyrus nevadensis* | Endurer (Rhizomes), Evader (Refractory Seed): 1,3 | 40 | 39 | 0 | 0 | 0 | 0 |
| *Polemonium viscosum* | Evader: 1 | 14 | 8 | 0 | 0 | 0 | 0 |
| *Smilacina stellata* | Endurer (Rhizomes): 1,3 | 0.75 | 0.75 | 0 | 0 | 0 | 0 |
| *Taraxacum officinale* | Invader (Wind Borne Seed): 1 | 0.75 | 0 | 0 | 0 | 0 | 0 |
| *Vicia americana* | Evader (Refractory Seed): 1 | 2 | 5 | 0 | 0 | 0 | 0 |
| *Dactylis glomerata* | Invader: 1 | 0.75 | 0 | 0 | 0 | 0 | 0 |
| *Phleum pratense* | Invader: 1 | 6 | 2 | 0 | 0 | 0 | 0 |
| *Ceanothus velutinus* | Endurer (Basal Sprouting), Evader (Refractory Seed): 1,2,3,4 | 5 | 3 | 0 | 0.75 | 0 | 0 |
| *Holodiscus discolor* | Endurer (Basal Sprouting): 1,2,3 | 13 | 11 | 0.75 | 0.75 | 0 | 0 |

| SPECIES | FIRE GUILD, LITERATURE CITATION | SR 92 | SR 93 | PSR 92 | PSR 93 | UB 92 | UB 93 |
|---|---|---|---|---|---|---|---|
| *Ribes cereum* | Endurer (Sprouting), Evader (Seed Bank Storage): 1,3 | 4 | 3 | 2 | 7 | 0 | 0 |
| *Ribes viscosissimum* | Endurer (Sprouting), Evader (Seed Bank Storage): 1,3 | 3 | 2 | 2 | 2 | 0 | 0 |
| *Rubus parviflorus* | Endurer (Rhizomes), Evader (Seed Bank Storage): 1,2 | 3 | 7 | 0.75 | 0 | 0 | 0 |
| *Sambucus racemosa* | Endurer (Basal Sprouting): 1,2 | 0 | 2 | 2 | 5 | 0 | 0 |
| *Salix scouleriana* | Endurer (Sprouting), Invader (Wind Borne Seed): 1,2,3 | 84 | 80 | 12 | 7 | 0 | 0 |
| *Spirea betulifolia* | Endurer (Basal Sprouting, Rhizomes): 1,3 | 13 | 16 | 0 | 25 | 0 | 0 |
| *Achillea millefolium* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1,3 | 16 | 17 | 12 | 13 | 0 | 0 |
| *Agoseris glauca* | Invader (Wind Borne Seed): 1 | 0 | 0.75 | 0.75 | 5 | 0 | 0 |
| *Anaphilis margaritacea* | Invader (Wind Borne Seed): 1,2 | 0 | 3 | 0 | 0.75 | 0 | 0 |
| *Antennaria microphylla* | Invader: 2 | 0.75 | 0 | 0 | 3 | 0 | 0 |
| *Aquilegia flavescens* | Endurer (Taproot): 1 | 0 | 0.75 | 5 | 18 | 0 | 0 |
| *Arnica cordifolia* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1,3 | 3 | 10 | 4 | 8 | 0 | 0 |
| *Aster conspicuous* | Endurer (Rhizomes): 1,3 | 8 | 5 | 2 | 3 | 0 | 0 |
| *Castilleja miniata* | Endurer (Rhizomes), Invader: 1,2 | 0 | 2 | 0 | 2 | 0 | 0 |
| *Cirsium vulgare* | Invader (Wind Born Seed): 2 | 0.75 | 0 | 3 | 2 | 0 | 0 |
| *Epilobium angustifolium* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1,3,4 | 66 | 67 | 26 | 32 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Epilobium minutum* | Invader (Wind Borne Seed): 1,3,4 | 22 | 22 | 0 | 7 | 0 | 0 |
| *Epilobium paniculatum* | Invader (Wind Borne Seed): 1,4 | 20 | 0 | 10 | 0 | 0 | 0 |
| *Eriogonum heracleoides* | Endurer (Root Crown): 1 | 2 | 0 | 0.75 | 0 | 0 | 0 |
| *Galium triflorum* | Endurer (Rhizomes), Invader (Animal Transport): 1,2,3 | 2 | 0 | 14 | 16 | 0 | 0 |
| *Gnaphalium microcephalum* | Invader (Wind Borne Seed): 1 | 0.75 | 0 | 3 | 0 | 0 | 0 |
| *Hieracium albertinum* | Endurer (Rhizomes), Invader (Wind Borne Seed):1 | 0 | 6 | 3 | 18 | 0 | 0 |
| *Iliamna rivularis* | Endurer (Caudex, Flower Stimulated Flowering): 1,2 | 0.75 | 2 | 0 | 2 | 0 | 0 |
| *Montia perfoliata* | Evaders: 1 | 0.75 | 0 | 13 | 19 | 0 | 0 |
| *Phacelia hastata* | Endurer (Caudex): 1 | 0 | 0.75 | 3 | 3 | 0 | 0 |
| *Potentilla glandulosa* | Endurer (Taproot): 1,3 | 3 | 0 | 9 | 5 | 0 | 0 |
| *Solidago canadensis* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1,2 | 3 | 7 | 0 | 4 | 0 | 0 |
| *Tonella floribunda* | Invader: 1 | 0 | 3 | 0 | 9 | 0 | 0 |
| *Stipa occidentalis* | Endurer (Root Crown): 1 | 3 | 0 | 0 | 0.75 | 0 | 0 |
| *Berberis repens* | Endurer (Rhizomes): 1,3 | 0 | 0 | 0.75 | 0 | 0 | 0 |
| *Lonicera utahensis* | Endurer (Basal Sprouting): 1,2 | 0 | 0 | 5 | 0.75 | 0 | 0 |
| *Ribes lacustre* | Endurer (Basal Sprouting): 1,3 | 0 | 0 | 0.75 | 0.75 | 0 | 0 |
| *Cryptantha torreyana* | Invader (Wind Borne Seed): 1 | 0 | 0 | 4 | 0 | 0 | 0 |
| *Erythronium grandiflorum* | Endurer (Taproot): 1 | 0 | 0 | 8 | 3 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Goodyera oblongifolia* | Endurer (Rhizomes): 1 | 0 | 0 | 2 | 0.75 | 0 | 0 |
| *Hackelia floribunda* | Endurer (Taproot), Invader (Animal Transport): 1 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Helianthella uniflora* | Endurer (Taproot), Invader: 1 | 0 | 0 | 0.75 | 0 | 0 | 0 |
| *Hieracium albiflorum* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1 | 0 | 0 | 0.75 | 5 | 0 | 0 |
| *Juncus parryi* | Endurer (Rhizomes): 1 | 0 | 0 | 0 | 0.75 | 0 | 0 |
| *Mertensia paniculata* | Endurer (Caudex): 1 | 0 | 0 | 10 | 13 | 0 | 0 |
| *Senecio triangularis* | Endurer (Rhizomes), Invader (Wind Borne Seed): 1,4 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Silene menziesii* | Invader: 1 | 0 | 0 | 0 | 8 | 0 | 0 |
| *Bromus carinatus* | Endurer (Root Crown): 1,4 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Trisetum spicatum* | Endurer (Root Crown): 1 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Agastache urticifolia* | Endurer (Caudex): 1 | 0 | 0 | 3 | 0 | 0.75 | 0 |
| *Aquilegia formosa* | Endurer (Taproot): 1 | 0 | 0 | 0.75 | 2 | 0.75 | 8 |
| *Sisymbrium altissimum* | Invader (Wind Borne Seed): 1 | 0 | 0 | 8 | 0 | 0 | 13 |
| *Urtica dioica* | Endurer (Rhizomes), Invader: 1 | 0 | 0 | 3 | 4 | 0.75 | 0 |
| *Calamagrostis rubescens* | Endurer (Rhizomes, Fire Stimulated Flowering): 1,3,4 | 0 | 0 | 3 | 0 | 2 | 4 |
| *Symphoricarpus albus* | Avoider (Rhizomes): 1,2 | 0 | 0 | 0 | 0 | 2 | 3 |
| *Vaccinium scoparium* | Avoider (Rhizomes): 3 | 0 | 0 | 0 | 0 | 0.75 | 0 |
| *Delphinium bicolor* | Avoider (Taproot): 1 | 0 | 0 | 0 | 0 | 0 | 13 |

| Disporum trachycarpum | Avoider (Rhizomes): 1,3 | 0 | 0 | 0 | 0 | 0.75 | 0 |
|---|---|---|---|---|---|---|---|
| Erodium cicutarium | Invader (Wind Borne Seed): 1 | 0 | 0 | 0 | 0 | 19 | 0 |
| Heuchera cylindrica | Avoider (Taproot): 2 | 0 | 0 | 0 | 0 | 2 | 0 |
| Senecio integerrimus | Invader (Wind Borne Seed): 1,4 | 0 | 0 | 0 | 0 | 0.75 | 0 |
| Trifolium longipes | Avoider (Rhizomes): 1 | 0 | 0 | 0 | 0 | 0.75 | 5 |
| Trillium ovatum | Avoider (Rhizomes, Corm): 1,2 | 0 | 0 | 0 | 0 | 0 | 0.75 |
| Veratrum californicum | Avoider (Rhizomes): 1 | 0 | 0 | 0 | 0 | 0 | 0.75 |
| Agrostis exarata | Invader: 2 | 0 | 0 | 0 | 0 | 6 | 0 |
| Abies grandis | Avoider: 1 | 2 | 4 | 10 | 9 | 17 | 23 |
| Abies lasiocarpa | Avoider: 1 | 0 | 0.75 | 5 | 0 | 11 | 0 |
| Larix occidentalis | Resister (Thick Bark): 1,4 | 0 | 4 | 25 | 9 | 13 | 2 |
| Pseudotsuga menziesii | Resister (Thick Bark), Avoider: 1,4 | 3 | 8 | 61 | 27 | 56 | 31 |
| Vaccinium globulare | Endurer (Basal Sprouting, Rhizomes), Avoider: 1,3 | 6 | 10 | 8 | 10 | 9 | 9 |
| Anemone piperi | Endurer (Rhizomes), Avoider: 1 | 39 | 43 | 40 | 24 | 8 | 10 |
| Arenaria macrophylla | Evader: 1 | 0 | 3 | 3 | 15 | 0.75 | 0 |
| Calochortus eurocarpus | Endurer (Fire Stimulated Flowering): 1,4 | 0.75 | 0 | 0 | 2 | 0.75 | 0 |
| Carex geyeri | Endurer (Rhizomes): 1,2,3 | 23 | 31 | 17 | 20 | 9 | 5 |
| Chimaphila umbellata | Endurer (Rhizomes): 2 | 3 | 3 | 0 | 11 | 3 | 4 |
| Collinsia parviflora | Evader (Seed Bank Storage): 2 | 0 | 9 | 0 | 27 | 0 | 8 |
| Cryptantha intermedia | Invader, Avoider: 1 | 3 | 5 | 2 | 3 | 14 | 14 |

| *Frageria vesca* | Endurer (Caudex): 2 | 0 | 0.75 | 2 | 13 | 0 | 0.75 |
|---|---|---|---|---|---|---|---|
| *Galium aparine* | Invader (Animal Transport): 1 | 0 | 2 | 2 | 4 | 0 | 0.75 |
| *Hydrophyllum capitatum* | Invader: 1 | 0 | 0.75 | 0 | 0.75 | 0 | 25 |
| *Lactuca serriola* | Invader (Wind Borne Seed): 1,2 | 5 | 14 | 7 | 11 | 0.75 | 2 |
| *Lupinus caudatus* | Endurer (Woody Taproot), Evader (Refractory Seed): 1,4 | 4 | 21 | 11 | 14 | 0.75 | 0 |
| *Mitella breweri* | Invader: 1 | 0 | 3 | 5 | 9 | 0 | 0.75 |
| *Osmorhiza chilensis* | Endurer (Taproot, Fire Stimulated Flowering): 1,3 | 0.75 | 0 | 14 | 49 | 0 | 5 |
| *Penstemon rydbergii* | Endurer (Caudex): 1 | 4 | 0 | 6 | 0.75 | 0.75 | 0 |
| *Phlox longifolia* | Evader (Seed Bank Storage): 1 | 6 | 9 | 3 | 4 | 0.75 | 0 |
| *Polemonium pulcherrimum* | Evader (Seed Bank Storage), Avoider: 1 | 15 | 2 | 45 | 64 | 4 | 15 |
| *Polygonum douglasii* | Evader (Seed Bank Storage), Avoider: 2 | 23 | 22 | 9 | 13 | 8 | 4 |
| *Pyrola secunda* | Endurer (Rhizomes): 1,3 | 9 | 3 | 19 | 6 | 6 | 0.75 |
| *Silene oregana* | Evader (Seed Bank Storage), Avoider: 1 | 0.75 | 5 | 20 | 22 | 6 | 26 |
| *Thalictrum occidentalis* | Endurer (Rhizomes): 3 | 0 | 3 | 24 | 23 | 2 | 3 |
| *Tragopogon dubius* | Invader (Wind Borne Seed): 1 | 5 | 0.75 | 9 | 2 | 2 | 0 |
| *Valeriana sitchensis* | Endurer (Rhizomes), Avoider: 1 | 5 | 0 | 14 | 23 | 2 | 5 |
| *Viola canadensis* | Endurer (Rhizome/Taproot): 1 | 23 | 24 | 47 | 54 | 0.75 | 9 |
| *Bromus vulgaris* | Invader: 1 | 18 | 18 | 39 | 63 | 0 | 11 |

## Community Richness, Diversity, and Evenness

Plots within partial stand-replacement fires had the greatest species richness, stands which experienced severe stand-replacement fires had intermediate levels of species richness, while unburned communities exhibited the lowest species richness (Table II.3.). Overall species richness of the study was 106. Within individual stands, S ranged from 10 in an unburned plot to 40 in a partial stand-replacement forest. For all plots combined, S in the stand-replacing fire was 75, in the partial stand-replacement fire, S was 81, and in unburned forests, S was 46.

There were 14 species which occurred only in stand-replacement forests, 15 species which occurred only in partial stand-replacement forests, and 11 species which occurred exclusively in unburned forests. Thirty-one species were common between stand-replacement and partial stand-replacement fires, and 5 species were common between partial stand-replacement fires and unburned plots.

Mean species richness for partial stand-replacement sites averaged 36 for 1992 and 35 for 1993. The mean species richness for the stand-replacement sites considering both years was 27. An average of 29 plants per sampled stand were in plots in 1993, while in the stand-replacement fires only 26 plants per sampled stand were in plots in 1992. In communities of severe stand-replacement fire, more species were detected during sampling in 1993, which may have been attributable to an increase in precipitation or a continued shift in species composition. For the unburned communities, species richness was less than half that of the partial stand-

Table II.3.  Species richness (S), Evenness (J'), and Diversity (H') by community following the 1988 Eagle Bar Fire at the Payette National Forest, Idaho.  SR=Stand-Replacement Fire, PSR=Partial Stand-Replacement Fire.

| | Species Richness (S) | | Species Evenness (J') | | Species Diversity (H') | | Diversity Variance | |
|---|---|---|---|---|---|---|---|---|
| | 1992 | 1993 | 1992 | 1993 | 1992 | 1993 | 1992 | 1993 |
| **Tussel Ridge West S.R.** | 29 | 27 | .8419 | .8546 | 2.835 | 2.817 | .00124 | .00117 |
| **Tussel Ridge East S.R.** | 34 | 39 | .8503 | .8737 | 2.998 | 3.201 | .00110 | .00102 |
| **Grassy Ridge S.R.** | 16 | 21 | .8362 | .8242 | 2.318 | 2.509 | .00136 | .00148 |
| **Sheep Rock S.R.** | 26 | 27 | .8346 | .8731 | 2.719 | 2.878 | .00184 | .00117 |
| **Stand Replace. Means** | 26 (5) | 29 (6) | .8489 (.009) | .8564 (.017) | 2.717 (.20) | 2.851 (.19) | .00140 | .00121 |

Table II.3., Continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Tussel Ridge West PSR** | 35 | 35 | .8636 | .9080 | 3.071 | 3.228 | .00114  .00057 |
| **Tussel Ridge East PSR** | 40 | 39 | .8731 | .9175 | 3.221 | 3.361 | .00125  .00071 |
| **Kinney Point PSR** | 31 | 33 | .8902 | .8865 | 3.057 | 3.100 | .00082  .00090 |
| **Sheep Rock PSR** | 38 | 34 | .8679 | .8686 | 3.157 | 3.063 | .00122  .00094 |
| **Partial Stand Replace. Means** | 36 (3) | 35 (2) | .8737 (.0083) | .8952 (.0176) | 3.127 (.063) | 3.188 (.11) | .00111  .00078 |
| **Horse Mt. N Unburned** | 14 | 12 | .8320 | .9575 | 2.196 | 2.379 | .00268  .00109 |
| **Horse Mt. S Unburned** | 14 | 10 | .8517 | .8278 | 2.248 | 1.906 | .00394  .00405 |

Table II.3., Continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Sawpit Ck. S Unburned** | 14 | 18 | .8010 | .8845 | 2.114 | 2.556 | .00390 .00155 |
| **Sawpit Ck. N Unburned** | 18 | 17 | .7546 | .8761 | 2.181 | 2.482 | .00529 .00133 |
| **Unburned Means** | 15 (2) | 14 (3) | .8098 (.0320) .8865 (.0355) | | 2.185 (.037) 2.331 (.21) | | .00395 .00201 |
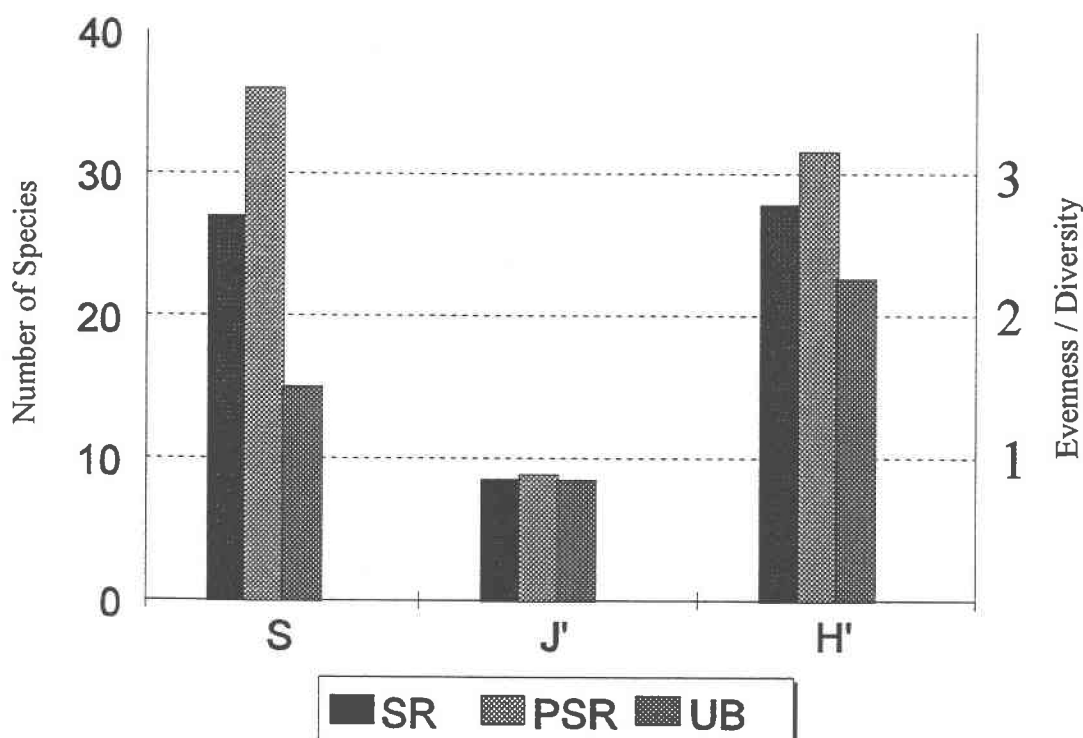
Figure II.1. Mean Species Richness, Evenness, and Diversity in Stand-Replacement (SR), Partial Stand-Replacement (PSR), and Unburned (UB) Forests in the Hells Canyon, Idaho for both years combined. S=Species Richness, J'=Species Evenness, and H'=Species Diversity.

replacement fire; S averaged 15 in 1992 and 14 in 1993. Species evenness, as a measure of the distribution of species within a community (Magurran 1988), ranged from 0.755 to 0.957 for all stands sampled (Table II.3., Figure II.1.). The mean species evenness for unburned communities was 0.848, while the mean species evenness for stand replacement sites was nearly identical, 0.849. Species evenness in

the partial stand-replacement fires was significantly greater than stand-replacement or

unburned forests, averaging 0.885 considering both years ($p < 0.05$).

Species diversity was significantly different among all fire scenarios

($p < 0.01$). Considering both years, partial stand-replacement forests had a

significantly higher diversity ($H' = 3.16$) than complete stand-replacement forests

($H' = 2.78$), which had a significantly greater diversity than unburned forests

($H' = 2.26$) (Table II.3.).

## Discussion

### Fire Guilds of Hells Canyon Forests

Because the Hells Canyon landscape has a disturbance history characterized with

several distinct fire regimes, endemic plants display a suite of ecological traits to survive

fire events in the particular habitats in which they survive. Fire survival traits are defined

as those adaptations that facilitate the survival of an individual or persistence of a species

(Kauffman 1990). Wildfire is a mechanism of natural selection in the evolution of life

forms; the biota must be distinctly adapted to fire regimes in which they exist (Pyne

1984). Studies of post-fire succession in this study as well as those in the Sundance Fire,

Idaho, (Stickney 1986), the Neal Canyon Fire, Montana, (Lyon 1971), and the Sleeping

Child Fire, Montana (Lyon and Stickney 1974) have revealed common guilds of

ecological adaptations that facilitate survival.

Traits facilitating the survival of the individual include basal sprouting in *Salix scouleriana* and *Lonicera utahensis* Wats. (Stickney 1986), and the thick bark of *Larix occidentalis* and *Pinus ponderosa* Dougl. (Kauffman 1990). These adaptations ensure individual survival of a single fire event.

In contrast to survival of the individual, certain ecological traits may enhance persistence of the species but not the individual. For example, *Pinus contorta* has arboreal seed storage in semi-serotinous cones which release seeds upon exposure to heat that is sufficient to kill the tree. *Epilobium paniculatum* and *Senecio triangularis* Hook. colonize burned areas from off-site, windborne propagules. *Ceanothus velutinus* and *Lupinus caudatus* have long-lived refractory seeds which germinate following scarification by fire (Kauffman 1990). Agee (1993) partitioned plants into fire guilds based upon adaptive traits to fire. In this study, we classified all plants into fire guilds of endurers, evaders, invaders, avoiders, and resisters (Table II.4.).

Invaders are characterized as highly mobile, pioneering species having propagules with short viability and survival (e.g., *Epilobium* spp., *Salix scouleriana*). Evaders are species having protected, long-lived propagules in arboreal or soil storage which are released or scarified following fire (e.g., *Pinus contorta, Ceanothus velutinus*). Avoiders are typically late successional species which colonize burned areas slowly and have limited ability to survive fire (e.g., *Abies lasiocarpa, Trillium ovatum* Pursh). Species with the capacity to sprout from aerial crowns, a root crown, taproots, or other subterranean organs are endurers (e.g., *Rosa gymnocarpa, Sorbus scopulina*). Species

which are protected from cambial damage from low-severity fires are classified as

resisters (e.g., *Pinus ponderosa, Larix occidentalis*) (Agee 1993, Kauffman 1990).

## **Fire Guild Distribution**

Of the 106 species present in the Eagle Bar Fire, 33% (n=35) were classified

as endurers. These species typically had larger, more sessile seeds, and relied

predominantly on vegetative regeneration for post-fire survival. *Carex geyeri,*

*Iliamna rivularis* (Dougl). Greene, *Aquilegia flavescens* Wats., and *Spirea betulifolia*

were endurers surviving through either rhizomes, caudexes, or taproots. Although these

species were capable of regenerating from seed, their dominant fire guild was the

capacity to endure top-kill through sprouting.

Species classified as invaders accounted for 24% of all plants detected (n=25).

Invaders were generally windborne immigrants which established from off-site sources,

such as *Agoseris glauca* (Pursh) Raf., *Crepis acuminata, Sisymbrium altissimum* L., and

*Anaphilis margaritacea* (L.) B. & H. Plants categorized as evaders comprised 7% of all

flora in the study (n=7). Evaders are those species capable of colonizing post-fire

environments through arboreal or refractory seed storage, such as *Pinus contorta, Vicia*

*americana, Collinsia parviflora* Lindl., and *Polygonum douglasii.*

Plants which were associated with late-seral conditions having essentially no

adaptation to survive fire (i.e., avoiders) represented 9% of the communities sampled

Table II.4. Common Fire Guilds and Survival Adaptations exhibited in the forests of the Hells Canyon, Idaho (after Agee 1993, and Kauffman 1990).

| ADAPTED TRAIT | FIRE GUILD (ENDURERS, EVADERS, INVADERS, AVOIDERS, AND RESISTERS) | ECOLOGICAL FUNCTION | SPECIES |
|---|---|---|---|
| Adventitious (Basal) Sprouting | Endurers | Vegetative regrowth following top-kill from subterranean root crowns | *Salix scouleriana, Sorbus scopulina, Rosa gymnocarpa, Acer glabrum, Lonicera utahensis* |
| Rhizomatous Sprouting | Endurers | Below ground lateral stem growth following fire | *Spirea betulifolia, Carex geyeri, Pyrola secunda, Rubus parviflorus, Smilacina* spp. |
| Thick Bark | Resisters | Insulates cambial tissue from damaging temperatures | *Pinus ponderosa, Larix occidentalis, Pseudotsuga menziesii* |
| Long-Term Refractory Seed Storage | Evaders | Provides long-term, viable seed in soil storage | *Ceanothus velutinus, Lupinus caudatus, Lathyrus nevadensis* |

Table II.4., Continued

| Windborne Seed Transport | Invaders | Saturating mineral-ash seedbeds with windborne seed | *Agoseris glauca, Salix scouleriana, Epilobium spp., Gnaphalium microcephalum, Anaphilis margaritacea, Senecio spp.* |
|---|---|---|---|
| Fire Stimulated Flowering | Endurers | Increased post-fire reproductive effort | *Calochortus eurocarpus, Calamagrostis rubescens* |
| Cone Semi-Serotiny | Evaders | Release of seeds from resin-sealed cones | *Pinus contorta* |
| Animal Seed Transport | Avoiders, Invaders | Seed transport from animal attachment, ingestion, or caching | *Galium aparine, Galium triflorum, Hackelia floribunda, Purshia tridentata* |

(n=10), and included *Trillium ovatum, Abies lasiocarpa, Delphinium bicolor,* and *Veratrum californicum* Durand.

*Larix occidentalis* was classified as a resister, having thick bark which protects cambial tissues from damaging temperatures. Certain species exhibit different fire guilds at different periods of their life. For example, *Pseudotsuga menziesii* is an avoider as a sapling and immature tree, but becomes a resister when thick bark develops later in life.

The remaining 28 species detected in the study exhibited duality of fire guilds. *Salix scouleriana* was classified as an invader due to its light, windborne seed, and as an endurer, due to its ability to sprout from buried root crowns. *Ceanothus velutinus, Lathyrus nevadensis, Ribes viscosissimum* Pursh, and *Lupinus caudatus* were classified as endurers and as evaders, due to their adaptations of sprouting and refractory seed storage. *Anemone piperi* and *Valeriana sitchensis* were categorized as endurers due to their ability to sprout from rhizomes, and as avoiders due to their occupancy in late-seral forests.

## Fire Guilds Within Fire Settings

The higher fire severity in the complete stand-replacement forests had several distinct effects. Not only did the complete stand-replacement fires result in proportionally fewer surviving species, but also in a proportionally greater colonization from both refractory (on-site) and off-site propagules. Unburned forests were

characterized by a smaller proportion of endurers and a greater proportion of species

categorized as avoiders than the other fire settings.

Severe stand-replacement fires were dominated by 33% endurers (n=25), 25%

invaders (n=19), 9% evaders (n=7), 11% endurers/invaders (n=8), and 22% species

having dual guilds (n=21) (Figure II.2.). In contrast, partial stand-
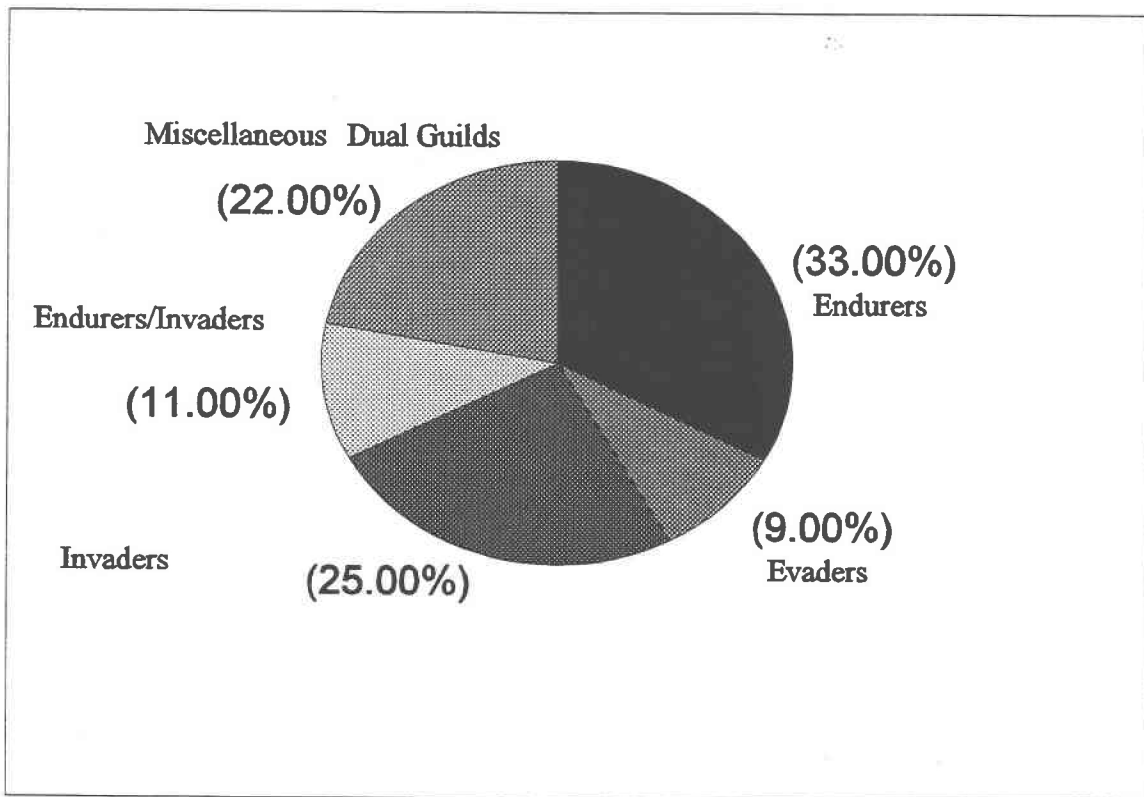


Figure II.2. Distribution of Fire Guilds Following Severe Stand-Replacement Fires at the Hells Canyon, Idaho.

replacement fires were comprised of 40% endurers (n=32), 5% evaders (n=4), 21%

invaders (n=17), 16% endurers/invaders (n=13), and 18% species exhibiting dual

guilds (n=15)(Figure II.3.). Unburned forests were dominated by 28% endurers

(n=13), 6% evaders (n=3), 22% invaders (n=10), 22% avoiders (n=10), 2%

resisters (n=1), and 20% by species having dual guilds (n=9).

Post-fire succession in burned forests relied more upon dual fire guilds than

that in unburned forests. Stand-replacement fires had the greatest recruitment from

invaders and evaders, corresponding to the creation of a mineral-ash seedbed and
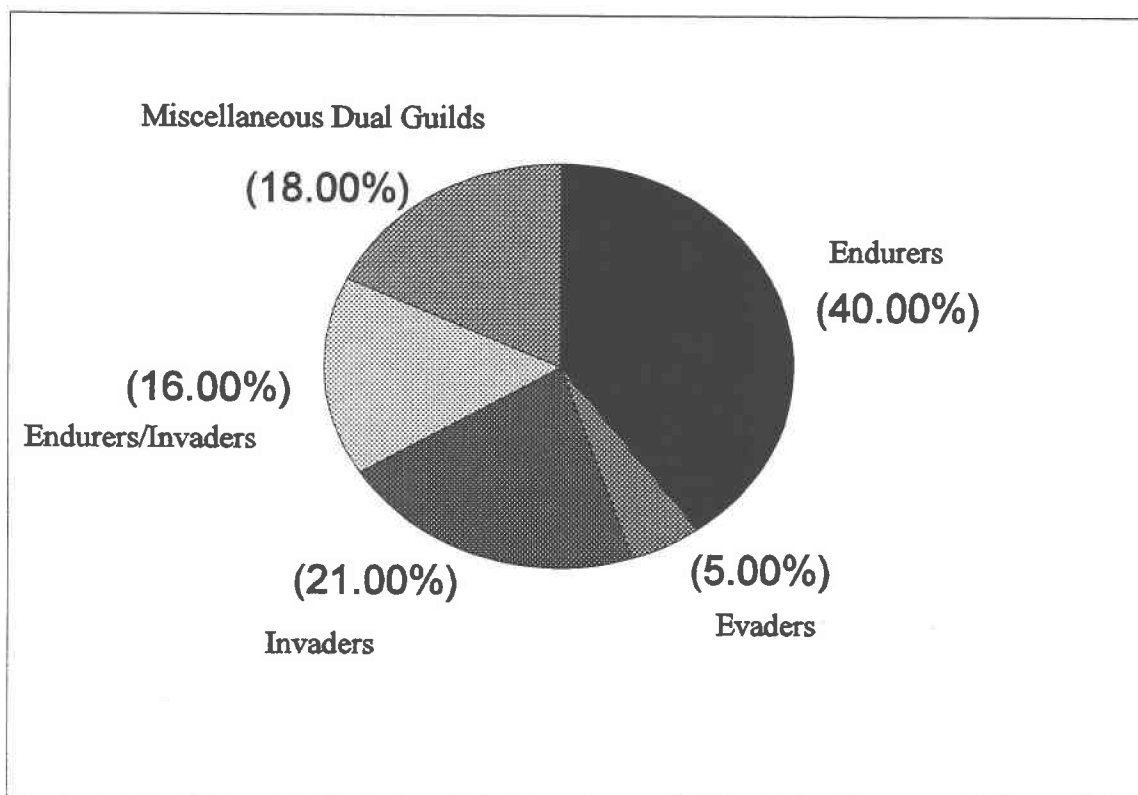


Figure II.3. Distribution of Fire Guilds Following Partial Stand-Replacement Fires in the
Hells Canyon, Idaho.

scarification of a refractory seed pool. Weatherspoon (1988) reported that a greater heat flux into the soil profile and complete consumption of the organic horizon resulted in a greater response from the refractory seed pool. Partial stand-replacement fires were characterized by the highest proportion of endurers, which resulted from a higher surviving proportion of the pre-fire community. Unburned forests were characterized by the highest number of avoiders (n=10) of any forest setting, due to late-seral conditions and the absence of recent fire in these forests.

## Disturbance Hypotheses

Fire severity not only influenced forest structure but also the preferential establishment of flora. A gradient of vegetation establishment was detected among the fire severity scenarios, as the distribution and composition of species were indicative of distinct fire regimes. Successional development in stand-replacement forests was characterized by a smaller proportion of surviving individuals, and greater recruitment from on-site and off-site propagules. Partial stand-replacement forests exhibited the highest species richness, evenness, and diversity, having the most species and the most uniform distribution of those species. Partial and complete stand-replacement fires in turn contribute to biological diversity through creation of distinctly different successional pathways, each associated with a unique composition and distribution of species.

Ecological studies have recently challenged the uni-directional, "Clementsian" theory of vegetation succession (Agee 1993, Botkin 1990, Crane and Fischer 1986) in favor of a concept which recognizes the possibility of multiple successional pathways (Cattelina et al. 1979). Connell and Slatyer (1977) proposed that following disturbance, vegetation development follows one of three alternative models: (i) facilitation, (ii) tolerance, and (iii) inhibition.

The "intermediate disturbance hypothesis" (Connell 1978) stated that species diversity is higher when disturbances are intermediate on the scales of frequency, area, and intensity. The species distribution in the study area was found to closely conform to this hypothesis. Connell (1978) stated that gradients of species diversity exist according to the timing and severity of disturbance; fewer species exist at the ends of the disturbance gradient, while more species occur in between. Specifically, communities which are severely disturbed or are undisturbed will be characterized by lower species diversity. Disturbances which are very frequent or are rare in occurrence tend to lower species diversity. Conversely, habitats experiencing moderate severity disturbances at regular intervals are associated with the highest structural and biological diversity, and are situated between the two ends of the gradient (Connell 1978).

In the Hells Canyon landscapes, the contribution to biological diversity from moderately burned sites is profound. These forests represent the mid-range of the intermediate disturbance gradient, and reflect the highest post-fire structural complexity and species diversity. The role of fire in such forests is to make available resources and niches for establishment, thereby functioning under the tolerance model (Connell and

Slatyer 1977). In contrast, complete stand-replacement forests are characterized as occupying one end of the disturbance gradient. Such sites which experiencing infrequent, high severity fires may exhibit lower biological diversity and niche width. Associated with stand-replacement fires is the recruitment of vegetation which functions under the inhibition model, thereby maintaining site dominance for relatively long periods (Connell and Slatyer 1977). Stand-replacement and unburned forests were located at opposite ends of this disturbance gradient. These forest scenarios had significantly lower species diversity (stand-replacement H'=2.78; unburned H'=2.26) than partial stand-replacement forests (H'=3.16) (p<0.01). The disturbance regime in partial stand-replacement fires represented a regular (60-100 year) perturbation typified by an intermediate severity disturbance. In these stands, the fire likely created a greater diversity of niches which in turn facilitated the immigration and establishment of the greatest number of species detected in any forest scenario.

In partial stand-replacement sites, fire has resulted in maintenance of floristic assemblages in a non-equilibrium state most closely associated with the "tolerance model" presented by Connell and Slatyer (1977). In this model, shifts in species composition occur according to the availability of resources and establishment sites resulting from disturbance. Compositional changes follow periodic disturbances which create niches for immigration, and the dynamic, non-equilibrium state of each assemblage does not facilitate or inhibit the development of successive communities (Connell and Slatyer 1977). As a dominant disturbance in this ecosystem, fire is largely

responsible for the creation of many niches and subsequently higher species diversity in partial stand-replacement forests.

In contrast, the post-fire floristic composition in complete stand-replacement forests corresponds to the "inhibition model" (Connell and Slatyer 1977). In this model of forest succession, a pulse of recruitment followed the severe disturbance, represented by *Salix scouleriana* and *Epilobium angustifolium*. These species then inhibited further compositional changes by their ability to exploit resources and occupy niches otherwise filled by a wide assemblage of flora. Concomitant with this site dominance were decreased species richness and a skewed distribution of species toward fewer, more dominant plants. In the inhibition model, successional advancement is often slow. In subalpine forest types, complete stand-replacement fires often result in shrub-dominated communities (Agee 1993), and on such sites, conifer establishment can be inhibited for over 40 years (Connell and Slatyer 1977).

## Multiple Successional Pathways

The variation in community composition in partial and complete stand-replacement fire communities exemplifies the multiple successional pathways which occur in the Hells Canyon landscapes. Community replacement sequences varied according to fire severity, pre-fire species composition, and fire frequency (Crane and Fischer 1986, Cattelina et al. 1979). Early successional theory of autogenic succession and relay floristics argued that plant succession advanced to a single climax community.

More recently, polyclimax theory has asserted that plant succession in tandem with disturbances result in mosaics of populations across environmental gradients, and that certain "climax" communities are tied to and dependent on disturbance for perpetuation (Agee 1993). In the Eagle Bar Fire, complete and partial stand-replacement fires created several potential successional pathways.

Two successional pathways were identified in complete stand-replacement forests, which were dominated by *Salix scouleriana* in the fourth and fifth post-fire years. The presence or absence of semi-serotinous *Pinus contorta* in the pre-fire community determined if *Pinus contorta* seedlings were in the post-fire community. At the Grassy Ridge and Sheep Rock sites, *Pinus contorta* seedling densities were 18,667 ha$^{-1}$ (SE=4,608) and 26,667 ha$^{-1}$ (SE=5,018) at the fifth post-fire year resulting from serotinous seed release after the fire. This successional pathway will likely lead to a replacement of the shrub community by *Pinus contorta* and eventually, *Abies lasiocarpa* (Agee 1993). Based upon observations in the study area, a lengthened fire-free interval in this community could advance to a mixed conifer forest of *Pseudotsuga menziesii*, *Abies grandis*, *Abies lasiocarpa*, and *Larix occidentalis* (Johnson and Simon 1987). However, if stand-replacing fire occurs while *Pinus contorta* remains an overstory dominant (i.e., within approximately 150 years), then the cycle of dominance from a *Salix scouleriana* to a *Pinus contorta* forest is probable (Agee 1993).

The Tussel Ridge stand-replacement sites had no established conifers, and no apparent trend away from this site dominance was detected during sampling. Although mean seedling density of *Salix scouleriana* decreased on these sites from 412,000 stems

ha$^{-1}$ (SE=62,343) to 348,000 stems ha$^{-1}$ (SE=42,554) from 1992 to 1993, *Salix scouleriana* was likely inhibiting the colonization of competing woody species at the fifth post-fire year. Based upon the duration of post-fire dominance of *Salix scouleriana* and *Ceanothus velutinus* in the 1960 Echels Creek Fire of the Hells Canyon, this shrub dominated community may persist for > 30 years.

Partial stand-replacement forests typify different successional pathways of mixed conifer forests. The resulting forest structure was characterized by unevenaged strata of dominant and suppressed trees. Fire events recruit a diverse assemblage of flora, including shade-tolerant conifers in the understory (Agee 1993). Relatively frequent fires on the scale of every 65-100 years kill the fire-intolerant understory and encourage an understory reinitiation stage (Agee 1993). This successional pathway was evident in partial stand-replacement sites which had a fire-tolerant overstory of *Pseudotsuga menziesii*; the mid-story of *Abies grandis* and *Abies lasiocarpa* were easily killed by fire. A forb-dominated understory of *Montia perfoliata* (Donn) Howell, *Mertensia paniculata* (Ait.) G. Don, and *Viola canadensis* was common at this point in succession. In the absence of fire, this multi-storied stand becomes predisposed to stand-replacement fire, after which entirely different successional pathways function. Under this successional pathway, sites which once supported a diverse forb community become dominated by *Salix scouleriana* and enter a phase of shrub dominance.

In the Hells Canyon ecosystems, the effects of fire are not spatially or temporally uniform. The variation in fire severity resulted in unique responses manifested in biological diversity and structural complexity. Because fire severity and timing have

great influences on seed pools and microsite conditions, these variables will interact to result in a variety of successional pathways for many decades to come.

## Forest Age Class and Fire Regime Classification

Within subalpine forests, pulsed conifer regeneration may follow severe fires, leading to single-story, even-aged stands (Agee 1993). In the study area, it is highly probable that most even-aged forests originated from this disturbance scenario. *Pinus contorta, Abies lasiocarpa, Abies grandis*, and *Pseudotsuga menziesii* were pre-fire conifers on the stand-replacement sites. The pre-fire age of these forests which were killed in the Eagle Bar Fire ranged from 99 to 159 years. These stand ages fall within the 100 to 300 year mean fire return interval typical of fire regimes of this forest type (Agee 1993). The mean pre-fire ages for the dominant conifers on three stand-replacement sites was 132 years (Sheep Rock, SE=3.46), 112 years (Grassy Ridge, SE=2.70), and 112 years (Tussel Ridge, SE=5.28) (Table II.5.). The density of *Pinus contorta* ranged from 80 stems ha$^{-1}$ (Sheep Rock) to 624 stems ha$^{-1}$ (Grassy Ridge), and diameter at 1.3 m (dbh) ranged from 7 to 58 cm. *Abies lasiocarpa* stand density ranged from 416 stems ha$^{-1}$ (Grassy Ridge) to 640 stems ha$^{-1}$ (Sheep Rock). The diameter ranged from 6 to 62 cm. The density of *Abies grandis*, only present at the Tussel Ridge West site, was 816 stems ha$^{-1}$. Diameter ranged from 3 to 39 cm. *Pseudotsuga menziesii* stand density ranged from 144 stems ha$^{-1}$ (Tussel Ridge West) to 256 stems ha$^{-1}$ (Tussel Ridge East). The diameter ranged from 13 to 106 cm.

A two-storied stand structure typified the forests experiencing partial stand replacement (Table II.5.). *Pseudotsuga menziesii* was the dominant overstory component, while *Larix occidentalis, Abies grandis, Pinus contorta,* and *Abies lasiocarpa* were present in the mid-story. In the partial stand-replacement forests, the density of *Abies lasiocarpa* ranged from 336 stems ha$^{-1}$ (Tussel Ridge East) to 656 stems ha$^{-1}$ (Tussel Ridge West), and diameter ranged from 2 to 40 cm. Density of *Abies grandis* ranged from 32 stems ha$^{-1}$ (Kinney Point) to 688 stems ha$^{-1}$ (Tussel Ridge East), and diameter ranged from 3 to 33 cm. The density of *Larix occidentalis* ranged from 64 stems ha$^{-1}$ (Sheep Rock) to 96 stems ha$^{-1}$ (Tussel Ridge West), while dbh ranged from 18 to 36 cm. *Pinus contorta* was present only at the Sheep Rock site. Stand density was 400 stems ha$^{-1}$, and the dbh ranged from 9 to 31 cm. *Pseudotsuga menziesii* survived in the overstory; density ranged from 128 stems ha$^{-1}$ (Tussel Ridge West) to 224 stems ha$^{-1}$ (Kinney Point). At these sites, diameter ranged from 80 to 130 cm.

The range in the age class distributions of these species suggests two distinct strata which were essentially even-aged. The range in ages of the midstory was 77 to 99 years, while the *Pseudotsuga menziesii* overstory age ranged from 165 to 209 years. The narrow window of ages within these strata are similar to that of Agee (1993, 1990) who also reported the presence of even-aged forest strata that were initiated following moderate-severity fires.

Trees in the unburned stands ranged from 59 to 167 years in age. The two Horse Mountain sites represented even-aged *Abies lasiocarpa* dominated forests

resulting from a severe fire event, with ages ranging from 59 to 87 years. The two

unburned plots in Sawpit Creek are late seral *Pseudotsuga menziesii* forests, ranging

from 84 to 167 years of age. The structural variation between the Horse Mountain

and the Sawpit sites appeared to be a legacy from an infrequent stand-replacing fire

regime in the former and a moderate severity, partial stand replacing fire regime in

the latter.

The primary fire regimes for subalpine, mixed conifer forests similar to those in

the study area have been characterized as infrequent, severe fire events with mean fire

return intervals ranging from 100 to over 200 years (Wellner 1970). However, data

from this study suggest that this may be a gross over-generalization because it ignores

the equally important moderate severity fire regime which has dramatically different

influences on long-term forest structure, biological diversity, and successional pathways.

The most widely studied fires in subalpine, mixed conifer forest ecosystems are

infrequent, high severity fires occurring on the order of 100 to > 300 years (i.e.,

complete stand-replacement fires) (Stickney 1986, 1990; Pyne 1984). Within this fire

regime, severe fire events cause complete aboveground mortality in forests dominated by

*Abies grandis, Abies lasiocarpa, Pinus contorta,* and *Pseudotsuga menziesii* (Johnson

and Simon 1987, Crane and Fischer 1986). Within such forests, the composition of early

seral stages is often dominated by shrub communities, notably *Salix scouleriana* and

*Ceanothus* spp. (this study, Stickney 1986). The rate and magnitude of conifer

regeneration appears dependent on seed availability from serotinous or wind-blown

sources (Agee 1993, this study, Stickney 1986). Within the sites experiencing

Table II.5. Stand Age Structure and Overstory Composition for subalpine forests in the Eagle Bar Fire at the Payette National Forest, Idaho. Mean age presented with standard error in parentheses.

| SITE | SPECIES | SAMPLE SIZE (n) | MEAN AGE (years) | RANGE IN AGES (years) |
|---|---|---|---|---|
| Sheep Rock Stand Replacement | *P. contorta*<br>*A. lasiocarpa* | 21<br>20 | 132 (3.46)<br>139 (3.44) | 100-155<br>101-159 |
| Grassy Ridge Stand Replacement | *P. contorta*<br>*A. lasiocarpa* | 20<br>20 | 112 (2.70)<br>119 (2.85) | 100-139<br>100-140 |
| Tussel Ridge East Stand Replacement | *P. menziesii* | 5 | 112 (5.28) | 99-129 |
| Tussel Ridge East Partial Stand Replacement | *P. menziesii*<br>*L. occidentalis* | 3<br>2 | 188 (11.26)<br>80 (2.50) | 169-208<br>77-82 |
| Tussel Ridge West Partial Stand Replacement | *P. menziesii*<br>*A. lasiocarpa* | 3<br>2 | 201 (4.30)<br>85 (7.00) | 194-209<br>78-92 |
| Kinney Point Partial Stand Replacement | *P. menziesii*<br>*A. lasiocarpa* | 3<br>2 | 184 (3.00)<br>80 (2.65) | 181-187<br>76-85 |
| Sheep Rock Partial Stand Replacement | *P. menziesii*<br>*L. occidentalis* | 3<br>2 | 172 (4.06)<br>91 (8.00) | 165-179<br>83-99 |
| Horse Mountain South Unburned | *A. lasiocarpa* | 5 | 73 (5.19) | 59-87 |

Table II.5., Continued

| Horse Mountain North Unburned | *A. lasiocarpa* | 5 | 71 (4.34) | 62-87 |
|---|---|---|---|---|
| Sawpit Creek South Unburned | *P. menziesii* | 5 | 125 (8.72) | 110-158 |
| Sawpit Creek North Unburned | *P. menziesii* | 5 | 123 (16.93) | 84-167 |

complete mortality, *Pinus contorta* was the only conifer establishing among an early seral community dominated by *Salix scouleriana*.

The moderate severity fire regime reported here has also been documented in the dry *Pseudotsuga menziesii* forests of the western Cascades, the mixed evergreen forests of southwestern Oregon, and the *Pinus contorta/Larix occidentalis* forests of Glacier National Park (Agee 1993, 1990; Barrett et al. 1991) . Within this fire regime, moderate severity fire frequency ranges from 25-100 years and results in a multi-aged stand with a diverse canopy structure. Associated with this intermediate severity fire regime, is an irregular, high severity fire regime on the order of 100 to >300 years, occurring under synoptic conditions, which results in complete overstory mortality and successional reinitiation. Surface fires in this regime are typified by mortality of the mid-strata conifers and the survival of the fire-resistant overstory (Agee 1990). Following fire, conifer seedlings are recruited in the understory (Agee 1993).

## Conclusion

Moderate and severe fire events had dramatically different influences on biological diversity, species composition and distribution, and forest age class structure in the Hells Canyon ecosystems. Post-fire succession was closely linked to the evolved ecological adaptations to fire in these communities.

A common fire regime, characterized by frequent partial overstory mortality and infrequent stand replacement, is an often overlooked but critical disturbance pattern in

the Hells Canyon. These mosaics resulting from partial post-fire mortality exhibited the greatest species richness, evenness, and diversity of the forest types sampled. Furthermore, these forests offered the greatest degree of structural diversity because of their uneven-aged nature.

Successional sequences were closely linked to fire severity. Complete, stand-replacement forests were dominated by *Salix scouleriana* and *Epilobium angustifolium*, while partial stand-replacement forests were dominated in the understory by a wide diversity of forbs such as *Silene oregana* and *Montia perfoliata*. Conifer regeneration (i.e., *Pinus contorta*) was detected only in those severely burned forests that experienced serotinous seed rain. In partial stand-replacement and unburned forests, *Pseudotsuga menziesii*, *Larix occidentalis*, and *Abies grandis* seedlings will likely dominate future successional development.

Due to the variations in fire severity and post-fire microclimate, multiple pathways of succession were occurring following the Eagle Bar Fire. In partial stand-replacement forests, the post-fire community was associated with the tolerance model (Connell and Slatyer 1977), in which diverse assemblages of flora follow regular, small scale disturbances. In this forest type, successional pathways are ultimately reinitiated from a complete stand-replacement fire after a lengthened fire-return interval. In contrast, post-fire succession in the complete-stand replacement forests was most closely correlated with the inhibition model (Connell and Slatyer 1977), in which several species successfully preempt site resources and maintain site-dominance until out-competed or becoming decadent. All stand-replacement sites (n=4) were dominated by *Salix*

*scouleriana* in the fifth post-fire year, and two such communities were advancing to *Pinus contorta* stands. The two remaining stand-replacement sites were dominated by *Salix scouleriana*; no trend away from this site occupancy was detected. These successional sequences following fire have profound impacts on long-term fire regimes and forest structure.

Vegetation in severely burned forests displayed highly evolved adaptations to fire. Refractory seed, cone serotiny, windblown seed, fire-enhanced flowering, and basal sprouting were common mechanisms for site reestablishment in forests experiencing high fire severity. Such forests relied heavily on invaders or evaders, which represented 9% and 25% of the post-fire community, respectively. Post-fire succession in partial stand-replacement forests was largely due to traits associated with individual survival, such as rhizomatous growth (*Viola canadensis*) and taproots (*Osmorhiza chilensis*) of endurers, which represented 40% of the post-fire community. Uneven-aged forests resulted from an intermediate, partial stand-replacement fire regime, characterized by *Pseudotsuga menziesii* in the overstory and *Abies lasiocarpa, Abies grandis,* and *Larix occidentalis* in the mid-story. Even-aged forests dominated by *Pinus contorta* and *Abies lasiocarpa* typified an infrequent, severe stand-replacement fire regime.

Associated with each fire regime are unique successional pathways and structural attributes, which in turn lend themselves to structural complexity on a landscape scale. This structural discontinuity at the landscape scale is typical for the forests of the Hells Canyon. As resource specialists attempt to manage for historic disturbance regimes,

continued fire is paramount in replicating patterns of regional biodiversity. Finally, the

concept of forest stability, often linked to biological diversity, appears to be enhanced,

not compromised, through fire as an ecosystem process.

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# CHAPTER III
## FIRE EFFECTS ON *Salix scouleriana* DEMOGRAPHY, BIOMASS, AND COVER IN STAND-REPLACEMENT FIRES OF THE HELLS CANYON, IDAHO

## Abstract

As a commonly occurring shrub throughout Idaho and the Pacific Northwest, Scouler willow (*Salix scouleriana* Barratt) is an important component in wildlife habitat, post-fire succession, and landscape diversity (Uchytil 1989). Throughout much of its range, *S. scouleriana* exists in a fire regime characterized by infrequent, high severity fire events. Therefore, this species must possess ecological traits insuring survival in fire-dominated ecosystems. The effects of two fire scenarios on the population dynamics of *S. scouleriana* were investigated in subalpine, mixed conifer forests in the Hells Canyon, Idaho. The fire scenarios included: (1) severe stand-replacement fire (complete overstory mortality); (2) partial stand-replacement fire (partial overstory mortality), and; (3) unburned areas within the fire perimeter. Seedling recruitment of *S. scouleriana* only occurred in areas of severe and complete stand-replacement fires. In the severe stand-replacement fires, this species completely dominated the early seral community. Density was 336,667 seedlings ha$^{-1}$ in 1992 and 246,000 seedlings ha$^{-1}$ in 1993. The removal of the organic horizon (creation of a mineral seedbed) and an altered microclimate resulting from the severe fire event appeared to facilitate the recruitment and initial site dominance of *S. scouleriana* in

the early seral communities. The dynamics of biomass, mean height, canopy cover, frequency of occurrence, and density of *S. scouleriana* were quantified from the fourth to the fifth post-fire year. During this time, *S. scouleriana* canopy cover increased from 30 to 37% while seedling frequency decreased from 83.5 to 80%. Mean biomass increased from 10 g to 33 g/seedling, and mean height increased from 62 cm to 100 cm/seedling. The increases in mean biomass and height and the decrease in seedling density of *S. scouleriana* at the fifth post-fire year suggest that interspecific competition and self-thinning in the willow community was occurring. The presence and duration of this shrub-dominated seral stage have strong implications regarding future forest structure and successional pathways in these sites valued for wildlife habitat, landscape diversity, and the continuation of historic processes. This study in concert with others (Stickney 1986, Lyon and Stickney 1974) suggests that *S. scouleriana* may dominate a site for decades without post-fire conifer establishment, with concomitant effects on long-term forest structure.

## Introduction

Forests of the Intermountain Region and the Northern Rockies evolved with fire as a pervasive ecosystem process (Pyne 1984). Fires from anthropogenic sources and lightning greatly influenced the composition and juxtaposition of various seral communities, creating structural heterogeneity on a landscape scale (Lyon and Stickney 1974). Many forests of the Intermountain and Northern Rocky Mountain

ecosystems are typified by a fire regime of infrequent, severe stand-replacement fires

resulting in even-aged mosaics across a heterogeneous landscape (Stickney 1986,

Lyon and Stickney 1974).

The two genera *Salix* and *Populus*, which collectively constitute the Salicaceae

family present in the region, are comprised of trees and shrubs which exhibit a

pronounced ability to survive in fire-dominated ecosystems (Foote 1983, Kauffman

1990, Stickney 1986). Periodic fire is necessary for the maintenance and

rejuvenation of quaking aspen (*Populus tremuloides* Michx.) forests by initiating

sprouting and suckering, and preventing successional advancement to conifer types

(Gordon 1974). Similarly, sprouting and seedling recruitment of Bebb willow (*Salix*

*bebbiana* Sarg.) in forested communities are largely dependent on periodic fires

(Foote 1983).

Scouler willow (*Salix scouleriana* Barratt), also known as fire willow, is a

common shrub in rangeland and forested settings throughout the Wallowa-Snake

Physiographic Province in eastern Oregon and west-central Idaho (Hitchcock and

Cronquist 1973). It occupies both riparian and upland communities, although it is

unique in being one of only two willows which consistently establishes on upland sites

in the western United States (Uchytil 1989, Brunsfield 1991). In the Hells Canyon,

*S. scouleriana* is an important browse component for resident deer and elk

populations (Jeffries, Personal Communication 1992).

Several attributes of the morphology and seed dispersal habits of *S.*

*scouleriana* enable it to colonize and at times dominate sites following severe fire

events (Uchytil 1989). *S. scouleriana* exhibits sprouting from adventitious buds located on root crowns buried beneath the soil surface (Stickney 1986). Following environmental disturbances, basal sprouting occurs. Seeds of *S. scouleriana* are extremely light (14,236,000/kg), covered by silky hairs, and buoyant, making them uniquely adapted to disperse by wind or water (Uchytil 1989). *S. scouleriana* is a classic r-selected survival strategist, dispersing copious numbers of seed to reach a limited number of safe sites created by disturbance. After the seeds are dispersed they are nondormant and retain their viability for only a few days. Germination occurs within 12 to 24 hours following dispersal, however, provided a moist, mineral seedbed is reached (Brinkman 1974).

Severe disturbances in rangeland and forest ecosystems create the microenvironment required for *S. scouleriana* germination and subsequent establishment. Contemporary timber harvest practices can result in excessive competition from *S. scouleriana* in the regenerating forest (Steele and Geier-Hayes 1987). However, as an early successional dominant following natural disturbances, *S. scouleriana* also plays an important role by influencing the sequence and composition of future seral communities. Hence, understanding the autecology of *S. scouleriana* and its subsequent influence on successional pathways is warranted.

The population dynamics of *S. scouleriana* and its linkage to fire severity are important concerns to wildlife biologists and fire planners in the study area. By quantifying patterns of post-fire succession relating to forest structure and wildlife habitat, questions regarding willow ecology and forest development can more easily

be addressed. To better understand the ecological relationships between fire and *S. scouleriana*, the following study objectives were established: (1) quantify post-fire *S. scouleriana* seedling recruitment in the severely burned, partially burned, and unburned forest communities; (2) describe changes in *S. scouleriana* seedling density, height, and biomass in plots experiencing severe, stand-replacement fires; and (3) determine the frequency of occurrence and canopy cover of *S. scouleriana* in forests experiencing stand-replacement fire during the 1988 Eagle Bar Fire in the Hells Canyon, Idaho.

## Methods

Four stands which experienced severe, stand-replacement fire in the 1988 Eagle Bar Fire were sampled. These sites are located on the Council Ranger District, Payette National Forest, Idaho. Areas exhibiting complete overstory mortality, significant bark charring, and complete organic matter consumption were considered to have experienced stand-replacement fire (Martin and Sapsis 1991).

At each study site a 25 m X 25 m plot was established. Plots were located in subalpine, mixed conifer forests at 1525 m to 2200 m in the Hells Canyon. Plot boundaries were established by a 1.5 m fencepost at each corner. Within each 25 x 25 m "macroplot", 30 randomly located "microplots" were established. Six microplots were positioned along each of five transects within each macroplot (i.e., 30 total microplots). Each microplot was 50 cm x 50 cm in size. Plot locations were

selected following reconnaissance by researchers from Oregon State University. Criteria for site selection were uniformity in elevation, pre-fire forest structure, and aspect. These studies on the Eagle Bar Fire occurred from June through October 1992 and 1993.

The study area is characterized by short, warm summers, and long cold winters. The area receives approximately 102 cm of precipitation annually, with > 70% occurring as snow between November and March. The mean July temperature averages 12.2°C, the mean January temperature averages -10.0°C, and the mean annual temperature is 7.5°C (USDA, Hells Canyon NRA Environmental Impact Statement 1979).

## Data Collection

At each plot, mean height, above ground biomass, canopy cover, frequency, and seedling density of *S. scouleriana* were quantified. Frequency was defined as the % of occurrence noted at a site (e.g., a species occurring in 20 out of 30 microplots would have 66% frequency). For the height and biomass measurements, seedlings were randomly selected outside of the plot. A buffer area of 1 m outside of the plot boundaries was established within which destructive sampling occurred to avoid disturbing the community inside the plot. At each study site, the above ground height (cm) of 50 seedlings was recorded (n=200) for each year. Above ground biomass was quantified by randomly clipping 30 plants outside of each plot at the

ground surface, placing them in paper bags, oven drying the seedlings for 48 hr at 100°C, and weighing the oven dried samples. Seedling density was calculated by counting individual seedlings within each microplot. Canopy cover was quantified by measurement using a calibrated surface within each microplot.

The age of the overstory trees at the time of the fire was quantified through cross sectional analysis of the dead *Pinus contorta* Dougl. and *Abies lasiocarpa* (Hook.) Nutt. snags killed during the fire. Snags were felled, and the samples cut at ground level were then sanded on a belt sander and growth rings were counted. Basal area at each study site was determined by measuring the diameter at breast height (DBH) for all trees inside each macroplot, and converting them to basal area per tree.

## Study Sites

Based upon the species composition in the unburned sites, the pre-fire understory was comprised of forbs such as *Polemonium pulcherrimum* Hook., *Smilacina stellata* (L.) Desf., and *Aquilegia flavescens* Wats. Understory shrubs consisted of shrubs such as *Lonicera utahensis* Wats., *Vaccinium globulare* Rydb., and *Sorbus scopulina* Greene.

### Tussel Ridge Stand Replacement West

This site is located approximately 49 km northwest of Council, Idaho in T21N, R3W, Sec. 14, SW/NW. Soils are derived from Permian Triassic volcanic

parent materials, averaging 76-102 cm in depth. Surface soils are classified as a fine sandy loam. Mean precipitation ranges from 62-119 cm annually, predominantly as snow in the winter months (Payette NF Landtype Guide 1988). Mean elevation of the site is 1678 m. The plot occurs on slopes averaging 46% on a northwest aspect. Vegetation is dominated by *S. scouleriana, Lathyrus nevadensis* Wats., and *Epilobium angustifolium* L. in the understory. *Pinus contorta* and *Pseudotsuga menziesii* (Mirbel) Franco. snags comprised the overstory. Other species present included *Calamagrostis rubescens* Buckl.

Due to inaccessibility, stand age could not be ascertained. Mean basal area of the stand, based upon post-fire measurements, was 68.2 $m^2$ $ha^{-1}$. Stand stocking was 992 stems $ha^{-1}$.

### Tussel Ridge Stand Replacement East

This site is located approximately 49 km northwest of Council, Idaho, in T21N, R3W, Sec. 14, SE/NW., approximately one-half mile from the previous site. Mean elevation of the site is 1804 m. Physical features are as above. The plot occurs on a northwest aspect with a slopes averaging 59%. The site is dominated by *L. nevadensis, E. angustifolium, P. contorta*, and *S. scouleriana* in the understory, and *P. menziesii* and *P. contorta* snags in the overstory. Other species present included *Anemone piperi* Britt.

Stand age of surrounding *P. contorta* forests averaged 112 years. Mean basal area, based upon post-fire measurements of the stand, was 53.8 m$^2$ ha$^{-1}$. Stand stocking was 256 stems ha$^{-1}$.

## Grassy Ridge Stand Replacement

This site is located approximately 50 km northwest of Council, Idaho in T21N, R3W, Sec. 11, NW/SE. Elevation at the site averages 2036 m. Soils are derived from granitic parent materials, and average 61 to 122 cm in depth. Surface soils are classified as a fine sandy loam. Mean precipitation ranges from 62 to 119 cm annually, largely as snow during the winter months (Payette NF Landtype Guide 1988). The plot occurs on slopes averaging 22% having a northwest aspect.

Vegetation at the site was dominated by *S. scouleriana, E. angustifolium, P. contorta*, and *Polygonum douglasii* Greene. in the understory, and *Pinus contorta* and *Abies lasiocarpa* snags in the overstory. Other species present included *Lupinus caudatus* Kell. and *Epilobium paniculatum* Nutt.

Pre-fire stand ages of *P. contorta* and *A. lasiocarpa* averaged 112 and 120 years, respectively. Mean basal area of the stand, based upon post-fire measurements, was 62.4 m$^2$ ha$^{-1}$. Stand stocking was 896 stems ha$^{-1}$.

Table III.1. Summary of Forest Structure at four *Salix scouleriana* communities in the Hells Canyon, Idaho. Payette National Forest. Data in parentheses are standard error of the mean.

| | Tussel Ridge West | Tussel Ridge East | Grassy Ridge | Sheep Rock | Overall Mean |
|---|---|---|---|---|---|
| Dominant Pre-Fire Conifer | *Psme, Abgr* | *Psme, Abla* | *Pico, Abla* | *Pico, Abla* | NA |
| Mean Basal Area ($m^2 ha^{-1}$) | 68.20 | 58.30 | 62.40 | 45.50 | 58.60 (6.70) |
| Stems $ha^{-1}$ | 992 | 256 | 896 | 832 | 744 (244) |
| Mean Diameter (cm) | 19 | 47 | 25 | 24 | 29 (9) |
| Mean Pre-Fire Age (years) of dominant | NA | 112 | 112 | 132 | 119 (9) |
| Elevation (m) | 1678 | 1804 | 2036 | 1939 | 1864 |
| General Aspect | NW | NW | NW | N | NA |
| Slope (%) | 46 | 59 | 22 | 25 | 38 |

Table III.1., Continued

| Legal Location | T21N, R3W, sec 14, SW/NW | T21N, R3W, sec 14, SE/NW | T21N, R3W, sec 11, NW/SE | T21N, R3W, sec 2, NW/NE | NA |
|---|---|---|---|---|---|

## Sheep Rock Stand Replacement

This site is located approximately 51 km northwest of Council, Idaho T21N, R3W, Sec. 2, NW/NE. Mean elevation of the site is 1939 m. Physical features are similar to the Grassy Ridge study location. The plot occurs on slopes averaging 25% having a north aspect. The site is dominated by *S. scouleriana, E. angustifolium*, and *L. caudatus* in the understory, and *A. lasiocarpa* and *P. contorta* snags in the overstory. Other species present include *Pyrola secunda* L. and *Polemonium viscosum* Nutt.

Pre-fire stand ages for *P. contorta* and *A. lasiocarpa* averaged 132 and 140 years, respectively. Mean basal area, based upon post-fire measurements of the stand, was 45.5 $m^2$ $ha^{-1}$. Stand stocking was 832 stems $ha^{-1}$. A summary of site descriptions for each study area are presented in Table III.1.

## Statistical Analysis

The study sites and plot locations were established in a completely randomized design. All analyses were conducted using STATGRAPHICS statistical software. Comparisons of seedling biomass, mean height, frequency of occurrence, canopy cover, and density between years were made using the Student's t-test. Tests for significant differences among the different fire scenarios were analyzed using ANOVA (Analysis of Variance).

## Results

### Willow Frequency and Cover

Significant differences between years were detected for frequency of *S. scouleriana* seedling occurrence at the Sheep Rock site, and for canopy cover at the Sheep Rock, Tussel Ridge West, and Tussel Ridge East sites (p<.10). Frequency of occurrence ranged from 50 to 100% among all plots for both years. *S. scouleriana* density decreased from 1992 to 1993. *S. scouleriana* occurred in 84% of the microplots in 1992, while present in 80% of all microplots in 1993. Three of the four sites had increases in frequency in 1993 over 1992 which were not significantly different. However, the Sheep Rock site had a significantly lower frequency in 1993 than in 1992 (Figure III.1.).

While a decrease in the presence of individuals was occurring, there was a concomitant increase in the canopy cover of *S. scouleriana*. Stated another way, there was an increase in the leaf area (the vertical projection of leaves downward to an equivalent unit area of ground) per individual which more than compensated for that lost through natural mortality of individuals (Waring and Schlesinger 1985). Mean canopy cover was 30% in 1992 and increased to 37% in 1993 (Figure III.2.). This increase occurred despite a decrease in seedling density (Table III.2., Figure III.3.).
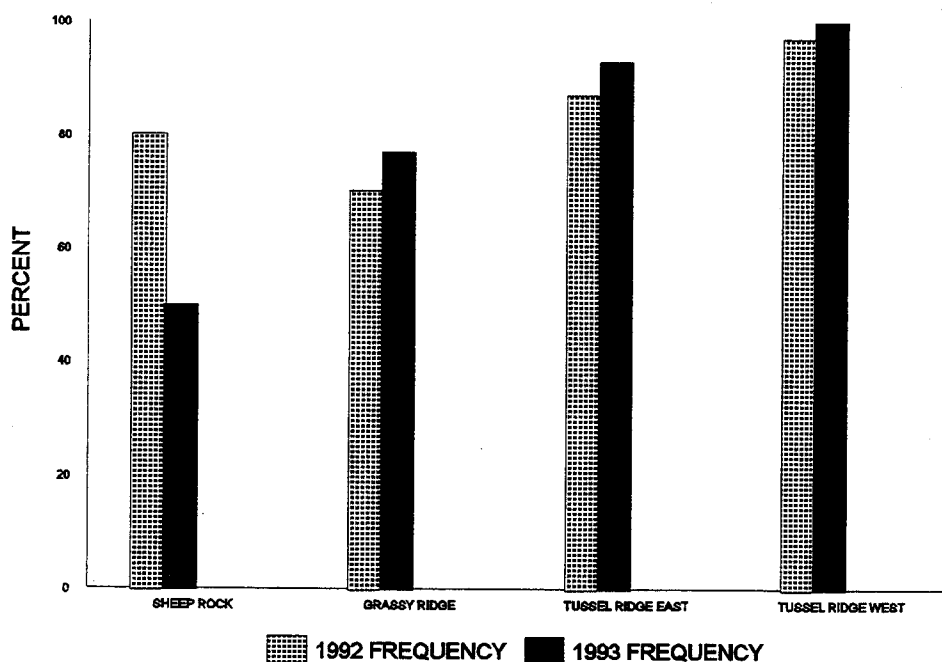
Figure III.1. *Salix scouleriana* frequency in the fourth and fifth post-fire years at the Hells Canyon, Idaho.

## Mean Height

In the fourth post-fire year (1992), mean height ranged from 52 cm (SE=2, Tussel Ridge West) to 70 cm (SE=3, Sheep Rock). Mean height ranged from 98 cm (SE=3, Sheep Rock and Tussel Ridge West) to 102 cm (SE=4, Grassy Ridge) in the fifth post-fire year (1993). The increase in mean height between the fourth and fifth

post-fire years showed significant differences (p < 0.10) at all sites. The magnitude of

increase varied from 40% at the Sheep Rock site to 88% at the Tussel Ridge West site

(Table III.2.).
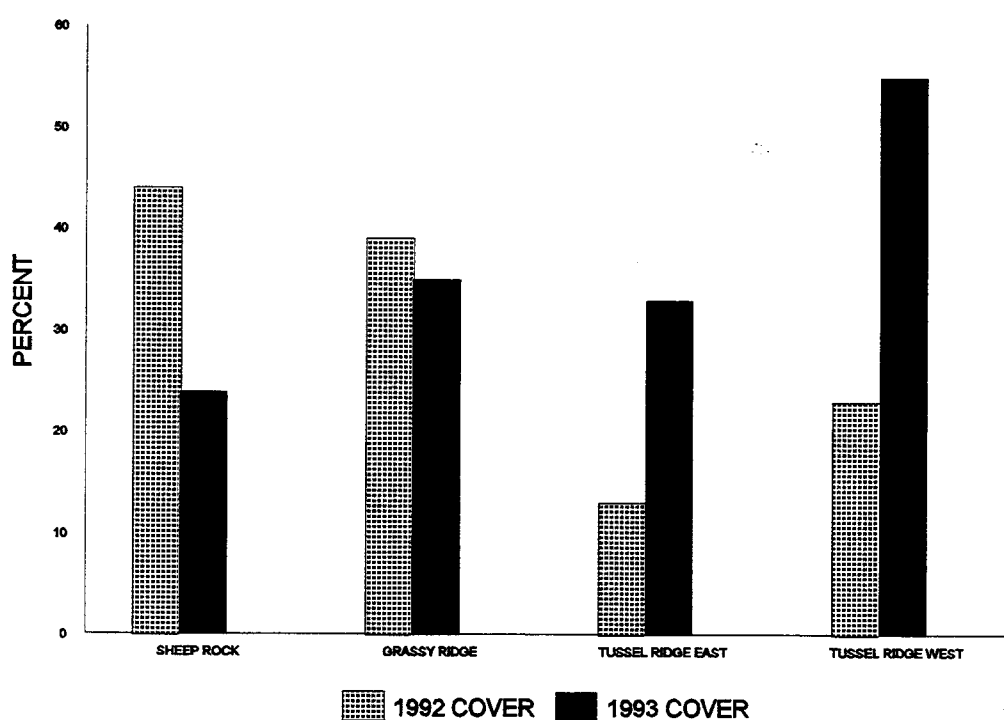


Figure III.2. *Salix scouleriana* canopy cover in the fourth and fifth post-fire years at the Hells Canyon, Idaho.

## Biomass

In the fourth post-fire year, mean above ground shrub biomass ranged from 3.55 g/shrub (Tussel Ridge West) to 17.14 g/shrub (Grassy Ridge). In the fifth post-

Table III.2. *Salix scouleriana* seedling density (seedlings ha$^{-1}$), biomass (g/seedling, Mg ha$^{-1}$), and mean height (cm) during the fourth and fifth post-fire years at the Payette National Forest, Idaho. Data area reported as means with standard errors in parentheses. n=30 samples per site.

| 1992 | Seedling Density (seedlings/ha) * | Mean Seedling Biomass (g) | Biomass (Mg ha$^{-1}$) | Height (cm) |
|---|---|---|---|---|
| Sheep Rock | 252,000[a] (53,808) | 13.99 | 3.53 | 70[a] (3) |
| Grassy Ridge | 270,667[a] (69,934) | 17.14 | 4.64 | 65[a] (3) |
| Tussel Ridge East | 254,667[a] (38,667) | 6.12 | 1.60 | 61[a] (3) |
| Tussel Ridge West | 569,333[a] (86,019) | 3.55 | 2.02 | 52[a] (2) |
| **MEAN** | 336,667[a] (62,107) | 10.20 | 2.95 | 62[a] (3) |
| **1993** | | | | |
| Sheep Rock | 121,333[b] (35,699) | 40.90 (3.70) | 4.96 (0.45) | 98[b] (3) |

| | | | | |
|---|---|---|---|---|
| Grassy Ridge | 166,667[b] (42,196) | 42.85 (3.35) | 7.14 (0.56) | 102[b] (4) |
| Tussel Ridge East | 208,000[b] (35,711) | 26.90 (2.33) | 5.60 (0.48) | 101[b] (3) |
| Tussel Ridge West | 488,000[b] (49,397) | 21.55 (1.37) | 10.51 (0.67) | 98[b] (3) |
| **MEAN** | 246,000[b] (40,750) | 33.05 (2.69) | 7.05 (0.54) | 100[b] (3) |

[*] Different superscripted letters denote a significant difference in seedling density and height between years ($p<0.10$).

fire year, mean above ground shrub biomass ranged from 21.55 (SE=1.37, Tussel Ridge West) to 42.85 (SE=3.35, Grassy Ridge) g/shrub. Expressed on an individual shrub basis, biomass at the Grassy Ridge site showed the smallest magnitude of change, where mean shrub biomass increased from 17.14 g/shrub in 1992 to 42.85 g/shrub in 1993. This corresponds to an increase in biomass from 4.64 Mg ha$^{-1}$ to 7.14 Mg ha$^{-1}$. Expressed on a biomass per ha basis, biomass at the Sheep Rock site showed the smallest increase among all plots, where mean above ground shrub biomass increased from 3.53 to 4.96 Mg ha$^{-1}$ (13.99 to 40.90 g/shrub). The greatest magnitude of increase in biomass occurred at the Tussel Ridge West site, where mean above ground biomass increased 600%, from 3.55 g/shrub to 21.55 g/shrub (2.02-10.51 Mg ha$^{-1}$).

## Seedling Density

Sites experiencing partial stand-replacement showed essentially no seedling

recruitment; *S. scouleriana* was detected in 11% of partial stand-replacement plots in

1992 and 7% of such plots in 1993. No *S. scouleriana* individuals were noted in

unburned forests. On severely burned sites, *S. scouleriana* plant density ranged from

121,333 ha$^{-1}$ (SE=35,699) to 569,333 ha$^{-1}$ (SE=86,019). Mean seedling density

decreased from 336,667 ha$^{-1}$ (SE=62,107) in 1992 to 246,000 ha$^{-1}$ (SE=40,750) in 1993

(Table III.2.). Significant differences were detected for the decrease in seedling density
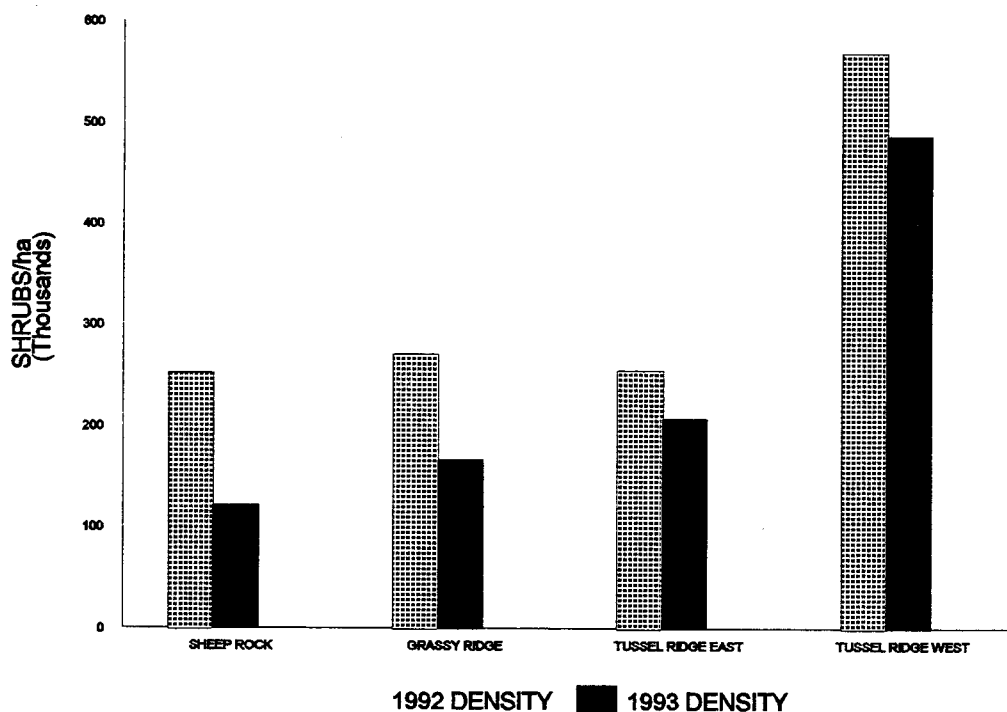


Figure III.3. *Salix scouleriana* seedling density in the fourth and fifth post-fire years at the Hells Canyon, Idaho.

at each of the four plots between the fourth and the fifth post-fire years (p<0.10). The

magnitude of seedling decrease noted from the fourth to the fifth post-fire years ranged

from 52% at the Sheep Rock site to 14% at the Tussel Ridge West site (Table III.2.).

The highest seedling density quantified was at the Tussel Ridge West site, where

569,333 seedlings ha$^{-1}$ were quantified in 1992. In 1993, seedling density decreased on

this site to 488,000 seedlings ha$^{-1}$ (SE=49,397). The Sheep Rock study area had the

lowest seedling density of all plots, experiencing a decrease from 252,000 to 121,333

seedlings ha$^{-1}$.

## Discussion

### *Salix scouleriana* Successional Pathways

The overall capacity of *S. scouleriana* to dominate sites following disturbance

appears to be in part linked to the amount of competition received from neighboring

plants. The trends in willow demography are potentially influenced by additional sources

of competition. In the pre-fire communities, *P. contorta* was a dominant conifer in the

overstory in the Sheep Rock and Grassy Ridge study areas. This tree is uniquely

adapted to fire events through long-term seed storage in serotinous cones. Periodic fires

which kill the individual tree also serve to release seeds stored in resinous, arboreal

cones on the branches. These seeds are then deposited on the mineral soil seedbed

resulting from the fire (Kauffman 1990).

Among all plots, the greatest mortality between years occurred at the Sheep Rock and Grassy Ridge study areas. Although a higher seedling density existed on the two Tussel Ridge study sites (and thus a higher probability for interspecific competition), they exhibited less mortality than the Sheep Rock and Grassy Ridge study areas. We hypothesize that the increase in canopy cover at the Tussel Ridge sites was strongly influenced by a lack of competing conifer saplings. In contrast, it appears that interspecific competition from *P. contorta* may have been a significant competitor with *S. scouleriana* at the Sheep Rock and Grassy Ridge sites which had decreases in canopy cover. The only significant change in frequency from 1992 to 1993 was at the Sheep Rock site, where shrub mortality resulted in a lower frequency of occurrence. The presence of *P. contorta* at the Sheep Rock and Grassy Ridge sites appeared to strongly influence decreases in seedling density and canopy cover.

Similar research was reported by Stickney (1986) in northern Idaho; *S. scouleriana* canopy cover continued to increase to approximately the fifth post-fire year, and among many plots to the tenth post-fire year. He concluded that an increase in canopy cover from competing shrubs or trees eventually limited the dominance of *S. scouleriana*. On the two study sites having competing *P. contorta* seedlings, *S. scouleriana* occurred in 69% of all microplots, while it was present in 94% of all microplots where *P. contorta* was absent.

Stickney (1986) described four pathways of succession involving *Salix scouleriana* following the 1967 Sundance Fire. Crane and Fischer (1986) projected multiple pathways of succession following fire in certain Idaho habitat types. Both

studies proposed that post-fire successional processes would depend on community composition, fire severity, and pre-fire disturbance regime. In the Eagle Bar Fire area, multiple pathways of succession are occurring in the first post-fire decade. At the Tussel Ridge sites, an extended period of *S. scouleriana* site dominance was noted without conifer regeneration. At the Grassy Ridge and Sheep Rock sites, an initial seral stage of *S. scouleriana* was being replaced by the next seral community of *P. contorta*. The resulting shrub and forest communities are distinctly different in terms of structure and long-term development.

The dramatic increases in *S. scouleriana* shrub densities from pre-fire to post-fire settings in these subalpine, mixed conifer forests are similar to findings by Stickney (1986) following the 1967 Sundance Fire in northern Idaho where it increased from an infrequent pre-fire shrub to a dominant shrub in the early post-fire communities. Similarly, Foote (1986) reported a post-fire *S. scouleriana* seedling density of 10,000 seedlings ha$^{-1}$ in Alaskan taiga forests. However, nowhere in the scientific literature could be found studies which have quantified a greater seedling density than those reported in this study (i.e., > 500,000 shrubs ha$^{-1}$ ).

Among all plots, decreases in shrub density were noted from the fourth to the fifth post-fire years. The presence of absence of *P. contorta* in early seral communities dominated by *S. scouleriana* appeared to have a competitive influence on trends in willow demography and succession. Dead and dying willow shrubs were typically suppressed and were being shaded out by taller, more robust willow individuals. Although the amount of canopy cover provided by *S. scouleriana* continued to increase

from the fourth to the fifth post-fire year, the absolute number of shrubs per unit area decreased. A similar pattern of shrub development was noted on the Sundance burn area (Stickney 1986).

Connell and Slatyer (1977) proposed 3 models (facilitation, tolerance, and inhibition) to explain the interaction between plant communities during successional development. The inhibition model stated that within certain communities, species will inhibit further successional advancement by dominating the site and its resources to the exclusion of all other species. This model best explains the early site dominance exhibited by *Salix scouleriana* in the Eagle Bar Fire area. Sites lacking *Pinus contorta* in the pre-fire community were completely dominated by *Salix scouleriana*, while those having post-fire seed deposition from arboreal *Pinus contorta* cones will likely enter a phase of shrub exclusion and conifer dominance. Agee (1993) stated that in similar high elevation conifer communities, sites could remain shrub-dominated for long periods if a conifer is not represented in the post-fire community. At the Grassy Ridge study site, there was an average of 16,000 *P. contorta* seedlings ha$^{-1}$ (SE=4479) in 1992. This increased to 18,667 (SE=4608) plants ha$^{-1}$ in 1993. At the Sheep Rock study area, *P. contorta* seedling density averaged 30,667 plants ha$^{-1}$ (SE=6127) in 1992, and decreased to 26,667 seedlings ha$^{-1}$ (SE=5,018). No *P. contorta* seedlings were noted on either of the Tussel Ridge sites. At the Grassy Ridge and Sheep Rock study sites, this additional source of competition may have resulted in a greater amount of mortality in the willow communities. This seral stage including *P. contorta* exemplifies the dramatic

role that cone serotiny in the pre-fire community composition may play on post-fire successional pathways.

Among all plots, the pronounced decrease in seedling density appears to be an example of density-dependent mortality (self-thinning). These findings support those of Harper (1977) when he reported that density stressed populations assume a bi-modal distribution, and that the risk of death is concentrated among the subordinate, suppressed strata.

Stickney (1986) reported that a common seral community following the Sundance Fire in northern Idaho was an "initial shrub stage sequence" dominated by *S. scouleriana* which existed through the tenth post-fire year. However, this community differed from those in the Eagle Bar Fire area because the willow community in the Sundance fire was composed of sprouting individuals, while those in the Eagle Bar fire were seedlings. Stickney stated that different early seral communities studied in the Sundance fire area exhibited minor recruitment of *S. scouleriana* seedlings, and that the only seral stage where this shrub was dominant was when it originated from a brushfield in the pre-fire community. As there were relatively few mature *S. scouleriana* plants in the pre-fire and unburned communities in the Eagle Bar Fire area, it can be concluded that the early seral shrub communities resulted predominantly from off-site seed sources and were distinct from those studied in the Sundance fire area.

Unburned islands were likely the seed source for willow establishment. The unburned *S. scouleriana* individuals adjacent to and inside the fire perimeter saturated the severely burned areas with windborne seed. Martin and Sapsis (1991) reported:

"...unburned islands are important as refugia for the biota from which they may repopulate the burned areas...The size, number, and distribution of unburned islands...will govern their effectiveness in restoring populations to the burned areas." According to Harper (1977), the recruitment of a seedling population is represented by an ecological sieve, which he defines as "an environmental lattice of safe and unsafe sites". Harper (1977) stated that seedling establishment is dependent upon encountering a safe site, consisting of: (1) sufficient water and oxygen resources; (2) the lack of environmental hazards (predators, competitors, toxic soils); and (3) favorable microtopographic features ensuring establishment. Harper (1977) suggested that recruitment of an even-aged class of cohorts occurred only after the seeds pass through such an ecological sieve. This concept of environmental sorting involves seeds surviving physical and chemical barriers before germination and eventual establishment (Harper 1977). Pre-fire inhibitors to successful colonization may include an organic horizon, competing vegetation, and toxic soils. Based upon the observations in this study, a safe site for *S. scouleriana* colonization may consist of a mineral soil seedbed, partial sunlight and standing dead woody debris, an elevational band between 700 to 2300 m, and a northwest aspect.

Species of the *Salix* genera have highly specific requirements for establishment from seed. Bussee (1989) reported that the distribution of Salicaceous species is dependent on the surface soil pH, mean organic matter content, organic horizon depth, and mean macroporosity. As are all willows, *S. scouleriana* is an r-selected survival strategist in that it produced copious amounts of seed which retain their viability for only

a few days and exhibit rapid germination following deposition on a moist, mineral seedbed (Uchytil 1989, Brinkman 1974). The population dynamics and stand structure of *S. scouleriana* are intimately linked to disturbance events, hence one common name "fire willow" (Uchytil 1989). In the Eagle Bar fire area, *S. scouleriana* seedlings differentially established in forests experiencing complete overstory mortality and removal of the organic horizon resulting from high fire severity. Associated with this alteration of microclimate were changes in the soil environment conducive to the germination and subsequent establishment of willow seedlings.

Although it is a highly fire-adapted species, *S. scouleriana* does not exhibit the dramatic seedling colonization, which was quantified in this study, across all of its range in North America following severe fire events. This raises the following questions: (1) what are the specific autecological requirements and fire adaptations of *S. scouleriana*, and; (2) what are the unique features of the Hells Canyon ecosystems, and what were the critical ecological mechanisms, influencing the population dynamics of *S. scouleriana*.

## Factors Affecting Seedling Establishment

The presence or absence of a residual organic horizon appeared to strongly influence the establishment *S. scouleriana*. An organic horizon was present in all partially burned and unburned plots. Only on sites experiencing the highest fire severity (indicated in part by exposed mineral soil conditions) was *S. scouleriana* recruited. It is also possible that the exposed mineral soil conditions had higher nutrient availability, an

altered pH, or fewer allelotoxins than the other fire treatments where willow establishment was inhibited (Harper 1977).

Aspect is another component of microtopography which appeared to influence *S. scouleriana* seedling establishment. North and northwest aspects had the greatest willow recruitment. Sites having east and south aspects had fewer seedlings than those quantified in this study, which were all on north-northwest aspects. This study suggests that moister conditions associated with north aspects contributed to greater recruitment of *S. scouleriana* than on southerly aspects.

Microclimate was an additional variable that may have influenced the magnitude of *S. scouleriana* colonization. In the study area, north facing slopes had greater conifer densities than south aspects. The partial (dead) shade offered by standing necromass more frequently encountered on north slopes appeared to contribute to the successful establishment of *S. scouleriana* seedlings. Conversely, full shade, such as that found in unburned forests, appeared to inhibit willow recruitment (Personal Observation). The presence of snags in the overstory has been observed to ameliorate the microclimate by increasing relative humidity, decreasing the proportion of direct sunlight, and influencing soil moisture conditions (Waring and Schlesinger 1985). Therefore, an important function of the residual standing woody debris is the alteration of the microclimate which will influence successional processes. As a result, the post-fire forest structure directly influenced *S. scouleriana* population dynamics.

In addition, elevation appeared to play a critical role in determining the prevalence of willow establishment. This was illustrated by contrasting the Tussel Ridge

West site with the Grassy Ridge site. In the former, the elevation was 1678 m and had

an average of 569,333 seedlings ha$^{-1}$ in 1992. In the latter, the elevation was 2036 m

and had an average of 270,667 seedlings ha$^{-1}$ in 1992. It appeared that the distribution

of the willows was normally distributed along an elevational gradient; no willows were

detected at the lowest elevations of the burn (512 m), and very few were present at the

highest elevations of the burn (2324 m). Conversely, those sites between elevations of

1600 and 1700 m exhibited the greatest seedling density. For example, the Tussel Ridge

West site was located at an elevation of 1678 m, and had a seedling density of 569,333

plants ha$^{-1}$ in 1992, the highest willow seedling density reported to date. This zone

appears to represent an ideal elevational band within which the greatest seedling

densities were quantified at the Hells Canyon. Hence, elevation, in addition to aspect,

seedbed conditions, microclimate, and seed availability, interact to determine the post-

fire distribution of *S. scouleriana* in the Hells Canyon.

## *Salix scouleriana* Fire Adaptations

*S. scouleriana* has evolved a variety of adaptations to survive in ecosystems

where fire is a repetitive ecological process. These adaptations can be categorized as

on-site and off-site adaptations (Lyon and Stickney 1974). On-site attributes are those

characteristics which enable an individual to survive a fire event, while off-site

adaptations are those traits allowing propagules (seeds or fruits) the mobility to colonize

or reestablish on a given area. Kauffman (1990) described fire adaptations as those

which facilitate the survival of the individual and those of the population. These ecological traits exhibited by *S. scouleriana* insure its survival within one historic fire regime of infrequent, severe stand replacement fires.

*S. scouleriana* has evolved two distinct adaptations to survive in fire dominated ecosystems. A primary fire adaptation exhibited by *S. scouleriana* is basal sprouting. Secondly, *S. scouleriana* populates post-fire environments through windborne seed (Stickney 1986). Plants displaying this reproductive plasticity in vegetative and sexual reestablishment are termed facultative (Kauffman 1990). Because of this ecological flexibility, the survival of either an individual or a population is not at risk from a single fire event. Basal sprouting is also the adaptation which may facilitate the survival of *S. scouleriana* from a shortened fire-return interval or several successive fires. Successive prescribed burns in northern Idaho to enhance elk (*Cervus elaphus*) habitat has resulted in sprouting of *S. scouleriana* following each fire (Leege 1968).

Basal sprouting originates from adventitious buds on root crowns buried beneath the soil surface. Lyon and Stickney (1974) stated that: "Root crowns represent the most important fire-survival adaptation for Northern Rocky Mountain shrubs". Although basal sprouting is an important element of fire survival for many shrubs, this statement may be an overgeneralization ignoring ecological traits of many species such as *Ceanothus* spp., *Cercocarpus ledifolius* Nutt., *Salix* spp., and *Artemisia tridentata* Nutt. which rely on sexual reproduction and windborne seed transport to survive fire events. The majority of shrubs in the northern Rocky Mountains are likely facultative sprouters, surviving fires by sprouting or from seed. Research by Wolff (1978), Foote

(1983), Leege (1968), and Lyon (1971) have quantified the magnitude of *S. scouleriana* basal sprouting and its relation to post-fire succession.

Observations on the Eagle Bar Fire indicate that the majority of mature *S. scouleriana* plants experiencing top-kill in the fire exhibited basal sprouting. Although there were approximately 25 sprouting *S. scouleriana* individuals ha$^{-1}$ in the post-fire community at the Tussel Ridge sites, the magnitude of *S. scouleriana* dominance was almost entirely due to seedlings, rather than sprouting individuals.

Within the Eagle Bar Fire area, the most striking dimension of the post-fire succession was the overwhelming dominance of *S. scouleriana* seedlings. This is a classic illustration of the r-selected survival strategy in the willow genera; there are 14,236,000 *S. scouleriana* seeds kg$^{-1}$ whose silky coverings aid in wind and water dispersal. As an off-site colonizer, *S. scouleriana* saturates sites with seeds and the resulting community can reflect the r-selected seed dispersal common in the Salicaceae family (Stickney 1986). Fire adaptations exhibited by woody plants in the Hells Canyon ecosystems include rhizomatous sprouting, thick bark, arboreal seed storage, and refractory seed storage (Table III.3.).

Discussing the ecology of *S. scouleriana,* Lyon and Stickney (1974) stated:

> Functional off-site species demonstrate adaptation to fire by their ability to introduce disseminules from areas well removed from the burn. Characteristically, these are lightweight airborne seeds or fruits...On the Sundance burn, reestablishment of...*Salix scouleriana* from root crowns was predictable, but an overwhelming saturation of airborne seed from this species has raised reestablishment percentages far above on-site expectation in early successional dominance.

Table III.3. Characteristics and ecological adaptations of woody plants to fire in the Hells Canyon,
Idaho (after Kauffman 1990, and Stickney 1986).

| ECOLOGICAL TRAIT | ON-SITE / OFF SITE ADAPTATION | FUNCTION | EXAMPLES |
|---|---|---|---|
| Adventitious (Basal) Sprouting | On-Site | Vegetative regrowth following top-kill from subterranean root crowns | *Salix scouleriana, Acer glabrum, Sorbus scopulina, Rosa gymnocarpa* |
| Rhizomatous Sprouting | On-Site | Below ground lateral stem growth following fire | *Vaccinium globulare, Physocarpus malvaceous, Spirea betulifolia* |
| Thick Bark | On-Site | Insulates cambial tissues from damaging temperatures | *Larix occidentalis, Pinus ponderosa, Pseudotsuga menziesii* |
| Arboreal Seed Storage | On-Site | Provides seed storage above soil | *Pinus contorta* |
| Long-Term Refractory Seed Storage | On-Site | Provides long-lived, viable seed in soil storage | *Ceanothus velutinus* |
| Windborne Seed | Off-Site | Saturating mineral-ash seed beds with off site seed | *Salix scouleriana* |

This ecological pattern of post-fire succession was distinctly illustrated on areas in the Eagle Bar Fire experiencing severe fire. Steele and Geier-Hayes (1987) reported that, "[*S. scouleriana*] windblown seed is most apt to establish on well-scarified soils". These findings support the observations in the Eagle Bar fire area, where a community dominated by *S. scouleriana* resulted from a severe fire event. First, the high severity wildfire, occurring in 1988, created the microsite conditions necessary for willow establishment. Windborne seed from nearby mature individuals in unburned areas dispersed seed in the spring of 1989. Following this dispersal and saturation of *S. scouleriana* seed onto the sites, a pulse of even-aged seedlings were recruited. Plots which were studied in adjacent areas experiencing moderate severity fire (plots experiencing partial overstory mortality and having a residual organic horizon) or which were unburned exhibited no seedling recruitment.

Explaining the origins and mechanisms influencing the development of the willow-dominated communities in this study requires some understanding of willow phenology (seed dispersal dates, windows of viability and germination) in relation to the time of the Eagle Bar fire. The fire burned during mid-August 1988, a time well past the phenological period of active seed dispersal and seedling establishment of willows. The period during which seed dispersal of *S. scouleriana* occurs in Montana, Utah, Wyoming and presumably Idaho is from April through June (Uchytil 1989). Although there were scattered sprouting *S. scouleriana* individuals on the sites in the spring of 1989 which were top-killed the previous summer, these sprouts were not phenologically mature and

were thus incapable of seed production (Personal Observation). Hence, the willow

community of interest established in the spring of 1989 from off-site seed sources.

## Conclusion

In this paper I have attempted to describe the population dynamics of *S. scouleriana* as it relates to fire severity, as well as quantify changes in five

seedling variables (mean height, density, biomass, frequency of occurrence, and canopy

cover) from the fourth to the fifth post-fire years. Willow-dominated communities

resulting from the 1988 Eagle Bar Fire were intensively sampled on four sites.

In the study area, forest mosaics are still created and maintained by fire events

which vary in space and time. Fire severity was found to directly influence the

recruitment of *S. scouleriana* seedlings by altering the soil environment, microclimate,

and competing vegetation. Sousa (1984) reported that as an agent of disturbance, fire

was responsible for spatial discontinuities in the distribution of populations, creating

small-scale patchworks of even-aged individuals. This ecological relationship is

strikingly apparent in the Hells Canyon ecosystems where vegetation mosaics testify to

the legacy of episodic fire events. Specifically, the even-aged communities dominated by

*S. scouleriana* seedlings following severe fire events strongly affect subsequent forest

development and successional pathways.

Shrub density decreased on all plots from the fourth to the fifth post-fire years

resulting from intra- and interspecific competition from *S. scouleriana* and *P. contorta*

seedlings, respectively. Those study sites having *P. contorta* in the pre-fire forest

exhibited pronounced *P. contorta* seedling recruitment in the post-fire community,

associated with concomitant decreases in willow shrub density, canopy cover, and

frequency. This corresponds to a seral stage eventually dominated by *P. contorta*, and a

continuation of the cyclic relationship between fire events and *P. contorta* recolonization

(Pyne 1984).

Mean height and biomass among *S. scouleriana* seedlings increased significantly

the fourth to the fifth post-fire year. While there was a decrease in seedling density,

surviving seedlings continued to increase in mean height and biomass. Further increases

in these two variables are expected during seral development associated with continued

decreases in seedling density.

In projecting the patterns of forest succession on these four study sites, the

presence or absence of conifer seedlings has direct implications regarding the next seral

community. Sites in the 1967 Sundance Fire of northern Idaho were dominated by *S.*

*scouleriana* for over one decade when conifer recruitment was lacking. The Tussel

Ridge sites exhibited a similar successional development, and may persist as long-term

shrub communities. Near the study sites, this is illustrated by a hillside dominated by *S.*

*scouleriana* and *Ceanothus velutinus* Dougl. originating from the Echels Creek wildfire

of 1960. At the time of the fire, the site was dominated by conifers, but 34 years later,

succession to a conifer-dominated community has not occurred (Personal Observation).

In contrast, it appears that a seral community of *P. contorta* will replace the *S.*

*scouleriana* dominated community on two of the four study areas. This likely structural

change from a shrub to a forest community will result from the presence of *P. contorta* in the pre-fire community. However, in the Tussel Ridge study areas lacking an immediate conifer seed rain following the fire, no established conifer seedlings were detected during sampling. Consequently, these sites could remain shrub dominated communities for at least 30 years based upon similar observations in the study area.

Basal sprouting and windborne seed, the latter a classic r-selected survival strategy, are the ecological adaptations which enable *S. scouleriana* to colonize and at times dominate areas following disturbance. In the subalpine, mixed conifer forests of the Hells Canyon, fire severity and subsequent alterations in microsite conditions directly influence patterns of secondary succession and community composition. Ideal site conditions contingent upon elevation, aspect, seed rain, and microtopography may contribute to early seral communities dominated by *S. scouleriana*. The presence and duration of this shrub-dominated community have direct implications regarding long-term forest structure, function, and successional pathways.

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# CHAPTER IV
## FIRE EFFECTS ON *Purshia tridentata* SURVIVAL RELATED TO AGE CLASS DISTRIBUTION IN THE HELLS CANYON, IDAHO

## Abstract

The survivorship of *Purshia tridentata* (Pursh) DC related to age class structure was investigated following the 1992 Windy Ridge Fire at the Payette National Forest, Idaho. Crown area, crown volume, age class distribution, and individual response to fire (i.e., sprouting and mortality) were quantified at 7 burned and 3 unburned plots dominated by *P. tridentata*, *Agropyron spicatum* (Pursh) Scribn. & Smith, and *Balsamorhiza sagittata* (Pursh) Nutt. A multiple regression model was constructed to predict plant age, and to test the hypothesis that post-fire survival was correlated with plant age. Mainstem basal diameter and shrub height were found to be the independent variables which best explained the variability associated with plant age ($R^2=0.70$). Following age predictions, individuals in the *P. tridentata* communities were partitioned into 5 year population segments. The mean age of all shrubs sampled was 27 years. Within the study area, the age of 25 years appeared to represent an ecological threshold beyond which *P. tridentata* dramatically declined in its capacity to sprout following fire. In age classes < 25 years, 66% of individuals sprouted; for age classes > 25 years, survival was 20%. The historic fire regime of a frequent fire-return interval for the Snake River grasslands maintained *P. tridentata* communities in younger age classes best suited to fire survival. High post-fire

mortality associated with a lengthened fire-return interval has resulted from successful fire control policies. In unburned stands, 5% of all individuals were dead. In burned communities, post-fire mortality averaged 74%, ranging from 37% to 100%. Considering all stands sampled, the overall age class distribution of *P. tridentata* was found to be bell-shaped, with very little recruitment occurring in the youngest age classes. It appears that an altered fire regime, associated with effective fire suppression, has created a shift in the age class distribution toward older, more decadent plants. As many *P. tridentata* stands in the western United States have reached decadent conditions resulting from a lengthened fire-free interval, future fire events may cause high levels of shrub mortality with little post-fire recruitment. In such communities, future fire events may well result in unnaturally high levels of shrub mortality, concomitant with alterations in vegetation diversity, winter range habitat, and long-term range structure.

## Introduction

Antelope bitterbrush (*Purshia tridentata* [Pursh] DC) is a common shrub throughout 10 million ha of the rangelands of the Pacific Northwest and the Great Basin. This shrub is considered to have a number of important values associated with wildlife habitat, nutrient cycling, and watershed stability (Tiedemann 1983). Due to the value of this Rosaceous shrub, research into many aspects of its ecology has occurred since 1900 (Eggler 1940, Smith 1952, Dickson 1953). However, research

addressing the historic and current role of fire in *P. tridentata* dominated ecosystems has often been inconclusive (Driver et al. 1980). The variability exhibited by *P. tridentata* is due in part to the diversity of environments is occupies; Franklin and Dyrness (1973) reported 18 habitat types in Oregon alone where it is a major component. Within these habitat types, historic fire regimes are characterized as frequent, low severity fire events which occurred every 5 to 50 years (Bradley 1986, Rice 1982).

Perhaps the greatest paradox regarding *P. tridentata* is the wide ecological amplitude noted in its reproductive traits, growth form, and fire responses. The variability has been hypothesized to be the reflection of a high level of ecotypic variation within the species (Nord 1965, Alderfer 1976, Driver 1980). It is now believed that *P. tridentata* occurs in specific ecotypes which display unique ecological responses to the environment (Nord 1965, Rice 1983, Martin and Driver 1983). The capacity to sprout following disturbance and growth form are understood to vary widely among soil type, age class, and physiographic location (Winward and Finley 1982). Such uncertainty can complicate management decisions relating to prescribed fire, wildlife habitat, and post-fire rehabilitation.

In the Hells Canyon, we tested the hypothesis that the capacity of *P. tridentata* to sprout following fire is related to fire severity and plant age. Previous research has found that *P. tridentata* sprouting ranged from 0 to > 90% (Clark 1979, Rice 1982). Driver et al. (1980) reported that post-fire sprouting ranged from 40-100% in a *Pinus ponderosa* Dougl./*P. tridentata* habitat type in Washington. Similarly, Blaisdell and

Mueggler (1953) reported that post-fire basal sprouting in eastern Idaho was significant in young plants experiencing low to moderate fire severity. In contrast, Countryman and Cornelius (1957) found that *P. tridentata* was removed from a community for over 6 years following burning in northeast California. Sherman and Chilcote (1972) reported minimal basal sprouting (< 1%) following fire in central Oregon *Pinus ponderosa* Dougl. forests.

Because *P. tridentata* occupies environments where frequent fires were historically common, we propose that this shrub has evolved ecological traits allowing it to survive within its historic fire regime. However, fire control policies of the last 50 years have altered fire frequency, and shifts toward older age classes have followed in many woody species (Pyne 1984). As a result of a decrease in fire occurrence, *P. tridentata* stands have experienced stagnation and decadence on a regional basis (Rice 1982). It appears that the survival adaptation of basal sprouting is compromised as plant age increases, leading to higher mortality in older ages classes.

To correlate post-fire survival with plant age, we have developed a two variable multiple regression model, using mainstem basal diameter and shrub height as independent variables. The population was partitioned into 5 year population segments at the time of the fire to examine the relationship between *P. tridentata* age class distribution and post-fire survival. The objectives of this study were to: (1) develop a multiple regression model to quantify the age class structure of 10 *P.*

*tridentata* communities; (2) examine post-fire survival and mortality rates of burned *P. tridentata* stands, and; (3) describe the linkage between age class and fire tolerance.

## Study Area

The Windy Ridge Fire burned 7,088 ha of the grasslands and mid-elevation forests of the Hells Canyon after starting on 19 August 1992. Plant communities which were burned at elevations between 570 m and 1300 m were dominated by *Agropyron spicatum* (Pursh) Scribn. & Smith, *Purshia tridentata*, *Prunus* spp., and *Pinus ponderosa*. Plots were established at 7 burned and 3 unburned sites distributed along an elevational gradient from 570 m to 1310 m. Eight plots were located on the Council Ranger District, Payette National Forest, Idaho, and 2 plots were established immediately across the Snake River in Oregon on the Baker Resource Area of the Bureau of Land Management.

A 25 m x 40 m plot (1/10th ha) was established at each study site. Each study site was representative of the *Purshia tridentata/Agropyron spicatum* (bitterbrush/bluebunch wheatgrass) plant association as described by Johnson (1987). Other species commonly occurring in this plant association include Sandberg's bluegrass (*Poa sandbergii* Vasey), arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.), fern-leaved lomatium (*Lomatium dissectum* [Nutt.] Math.&Const.),

and deer horn (*Clarkia pulchella* Pursh). Field work was conducted from June to August, 1993, the first post-fire year following the 1992 Windy Ridge Fire.

Burned and unburned *P. tridentata* communities were sampled in order to quantify differences in mortality among disturbed and undisturbed stands. Criteria for site selection were similarity among species composition, aspect, soils, and a range in elevations. All sites were on southwest, south, or southeast aspects, and located on shallow, well-drained skeletal soils. Pre-fire shrub density ranged from 400 to 1700 plants ha$^{-1}$ (Table IV.1.).

Tisdale (1986) described the area as having a semi-arid climate of hot, dry summers and cold winters. The mean July temperature averages 24°C, the mean January temperature averages 1°C, and the mean annual temperature is 11°C. Precipitation averages 450 mm annually, with the majority occurring from November to February as snow.

## Methods

All *P. tridentata* shrubs rooted within the ten 25 m x 40 m study plots were measured. Data from a total of 776 *P. tridentata* shrubs are included in this study. In addition to these measurements, plant age, the dependent variable in the model, was quantified from a subsample (n=80) to develop a regression model to predict age. Ages of plants were found to range from 4 to 68 years. Plant age was determined by cross-section analysis of the growth rings, taken where the mainstem

Table IV.1. Summary of *Purshia tridentata* communities sampled following the 1992 Windy Ridge Fire at the Payette National Forest, Idaho.

| SITE | ASPECT | ELEVATION (m) | LEGAL LOCATION | PREFIRE DENSITY (SHRUBS ha$^{-1}$) | SOIL TYPE |
|---|---|---|---|---|---|
| Snake River Burned | S | 573 | T20N, R4W, sec. 23, NW/SE | 1110 | Gravelly Clay Loam |
| Ballard Creek Unburned | SE | 586 | T6S, R48E, sec. 15, NE/NE | 830 | Gravelly Clay Loam |
| Snake River Burned II | SW | 787 | T20N, R4W, sec. 23, NE/SE | 720 | Gravelly Clay Loam |
| Snake River Burned III | S | 909 | T20N, R4W, sec. 23, SW/NE | 940 | Gravelly Clay Loam |
| Snake River Burned IV | S | 930 | T20N, R4W, sec. 23, NW/SW | 420 | Gravelly Clay Loam |
| Ross Basin Burned | SE | 1068 | T20N, R4W, sec. 13, SW/SW | 780 | Gravelly Sandy Clay Loam |

Table IV.1., Continued

| | | | | | |
|---|---|---|---|---|---|
| Upper Ross Basin Burned | S | 1098 | T20N, R4W, sec. 13, SE/SW | 400 | Gravelly Sandy Clay Loam |
| Upper Ross Basin Unburned | S | 1117 | T20N, R4W, sec. 24, NE/NW | 1170 | Gravelly Sandy Clay Loam |
| Windy Ridge Burned | SE | 1232 | T20N, R4W, sec. 25, SE/NW | 1700 | Sandy Loam |
| Indian Creek Unburned | SE | 1312 | T20N, R4W, sec. 24, NE/NE | 640 | Sandy Loam |

entered the soil surface. Basal diameter was ascertained by caliper measurement of the mainstem at the soil interface. For all *P. tridentata* shrubs within each macroplot, the following variables were measured: (1) plant height (cm); (2) basal diameter (cm); (3) plant status (i.e., live-unburned, dead-unburned, dead-burned, sprouting-burned); (4) elliptical crown area; and (5) crown volume. Elliptical crown area (A) was calculated utilizing the formula:

$$A = \frac{3.1415 * W_1 * W_2}{4}$$

where $W_1$ is the maximum diameter and $W_2$ is the perpendicular diameter to $W_1$. Crown volume (m$^3$/plant) was calculated by multiplying plant height by crown area.

## Shrub Partitioning

During sampling, shrubs were separated into the following categories: (1) individuals that were burned and killed; (2) those that were top-killed (crown mortality) but regenerated from basal or epicormic sprouts; (3) those which were unburned and dead; and (4) those which were unburned and live. From these data, fire-induced plant mortality (i.e., failure to resprout), plant mortality and survival among unburned stands, and the proportions of burned populations surviving through basal or epicormic sprouting at each study site were quantified. The size of individuals sampled ranged from seedlings less than 15 cm in height to individuals over 2.7 m in height.

Individuals at each study site were partitioned into the following age classes: 5-10 years; 10-15 years; 15-20 years; 20-25 years; 25-30 years; 30-35 years; 35-40 years;

40-45 years; and 45-50 years. Within each age class, the number of plants experiencing

sprouting or fire-induced mortality, and which were unburned were quantified. From

these data, estimates of post-fire sprouting and mortality were made within each age

class. These figures were then used to construct an age class distribution for each study

site and for the entire population sampled. Comparisons were then made between each

site regarding post-fire sprouting and patterns of mortality.

## Statistical Analysis

Stepwise multiple regression analysis was performed using STATGRAPHICS

statistical software to select the best-fit equation to predict age. Independent variables

which were tested to construct the multiple regression model included crown area,

crown volume, plant height, and mainstem basal diameter. Using stepwise selection

procedures, the best fit equation involved mainstem basal diameter and plant height as

the only explanatory variables. Logarithmic transformations were performed to all

variables to meet equal variance and linearity assumptions. The equation is presented in

the log-log form: $\ln(Y) = a + b*\ln(X_1) + c*\ln(X_2)$, where X's are the independent

(explanatory) variables of mainstem basal diameter and height. The variable "a"

represents the intercept of age in the model, and b and c are correlation coefficients.

Data were detransformed into the original units following the construction of the

predictive equation. However, detransformed values are estimates of the geometric

mean, rather than the arithmetic mean (Smith 1993), thereby incorporating an inherent

bias. To correct for detranformation bias, each predicted age was multiplied by the ratio estimator correction factor, as suggested by Snowdon (1991) and Smith (1993). The ratio estimator corrects detransformed predictions by multiplying them by the mean of the observed Y values divided by the mean of the detransformed predicted values. As a result, predictions of ages were slightly increased for these data.

Utilizing the multiple regression predictive equation, ages of 491 burned shrubs were predicted. The population sampled was then partitioned into 5 year age class segments, and a regression of % mortality on age class was performed in STATGRAPHICS.

## Results

### Study Site Comparisons

There was variation in the community and individual shrub parameters of density, mean height, and basal diameter among the 10 sampled sites, due mostly to minor differences in mean stand age. Parameters used in quantifying *P. tridentata* community structure are presented in Table IV.4. One parameter with a great range of variability was shrub density, which ranged from 400 to 1700 shrubs ha$^{-1}$. Mean shrub density was 871 shrubs ha$^{-1}$ (SE=122).

Mean height (cm) among sites ranged from 42 (SE=1) to 137 cm (SE=5). Mean height averaged 85 cm (SE=4). Mean age (years) ranged from 23 (SE=1.17) to 32 years

(SE=.66). The overall mean age considering all sites was 27 years (SE=.73). Mean mainstem basal diameter varied from 3.3 (SE=.12) to 7.8 cm (SE=.53). Among all sites, mainstem basal diameter averaged 5.3 cm (SE=.28).

Crown area ranged from 789 (SE=107.5) to 2650 $m^2$ $ha^{-1}$ (SE=201.5) among all 10 sites. These figures represent a range in canopy cover from 7.9 to 26.5%, respectively. Mean crown area for all sites was 1564 $m^2$ $ha^{-1}$ (SE=136.5) (15.6% canopy cover). Crown volume ($m^3$/plant), calculated by multiplying crown area by plant height, ranged from .32 $m^3$/plant (SE=.03) to 6 $m^3$/plant (SE=.30). This range is attributable to the fact that the former site (Windy Ridge Burned) was dominated by a greater density of younger plants which were smaller in size, while the latter site (Snake River Burned II) was comprised of an older stand having a lower shrub density, but a much greater mean shrub height and crown area. Mean crown volume considering all sites was 2.99 $m^3$/plant (SE=.24).

The area occupied by each shrub ($m^2$/plant) was calculated for each site, and ranged from 5.9 to 25 $m^2$/plant at the Windy Ridge Burned and Upper Ross Basin Burned sites. These values were density dependent (Table IV.2.).

Basal sprouting ranged from 0 to 58% on burned sites, and epicormic sprouting ranged from 0 to 2% on burned sites. Shrub mortality among burned communities ranged from 37 to 100%.

## _P. tridentata_ Age Class Distribution

Ages of 776 shrubs sampled ranged from 9 to 50 years. The age class

distribution of the _P. tridentata_ with all stands combined assumed a bell-shaped

distribution. Shrubs ranging in age from 20 to 35 years accounted for 67% of all shrubs

(n=521). Very few shrubs had recently established in the communities; there were 2

shrubs in the 0 to 10 year age class, while 4 shrubs were in the 45 to 50 year age class.

The mean age for all shrubs sampled was 27 years. Of the 607 individuals located

within burned plots, 16% (n=95) experienced complete above ground consumption

and were only distinguishable by a root crown at the soil surface. Among burned

sites, complete consumption ranged from 6 to 50% of all plants within the plot.

Conversely, 3.5% (n=21) of all shrubs within burned plots were not burned. In the

same plots, unburned individuals accounted for 0 to 14% of all shrubs. Limited fuel

continuity was most often the reason for patchiness in the pattern of burning.

_P. tridentata_ survival following fire was negatively correlated with plant age

($R^2$=0.91, p=.0001); shrub survival (basal and epicormic sprouting) decreased with

successive increases in age class (Figure IV.2.). Basal sprouting was the dominant form

of post-fire survival, accounting for 98% (n=159) of all sprouting. Epicormic sprouting

was only responsible for 2% (n=4) of all sprouting. Considering all shrubs which were

burned, 28% (n=163) exhibited either basal or epicormic sprouting. In contrast, 72%

(n=423) of all shrubs experiencing fire were killed.

Table IV.2. *Purshia tridentata* community parameters following the 1992 Windy Ridge Fire at the Payette National Forest, Idaho. Data are presented as means with standard errors in parentheses.

| | Ballard Creek UB | Upper Ross UB | Indian Creek UB | Unburn Mean | Ross Basin B | SR B I | SR B II | SR B III | SR B IV | Upper Ross B | Windy Ridge Burned | Burned Means |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sample Size (n) | 83 | 117 | 64 | 88 | 73 | 89 | 36 | 84 | 35 | 37 | 158 | 73 |
| Density (plants/ha) | 830 | 1170 | 640 | 880 | 780 | 1110 | 720 | 940 | 420 | 400 | 1700 | 867 |
| Density (m²/plant) | 12.05 | 8.55 | 15.63 | 11.36 | 12.82 | 9.01 | 13.89 | 10.64 | 23.81 | 25.00 | 5.88 | 11.53 |
| Mean height (cm) | 136.82 (5.37) | 58.59 (1.91) | 56.21 (4.71) | 83.87 (3.99) | 78.11 (6.49) | 122.51 (3.79) | 100.83 (8.04) | 109.89 (4.72) | 129.50 (7.99) | 98.22 (7.71) | 41.99 (1.34) | 97.29 (5.73) |
| Mean Basal Diameter (cm) | 7.08 (.32) | 3.59 (.14) | 3.81 (.35) | 4.83 (.27) | 4.85 (.39) | 7.66 (.29) | 5.58 (.51) | 7.14 (.32) | 7.82 (.53) | 6.05 (.46) | 3.31 (.12) | 6.06 (.37) |
| Mean Age (Years) | 29.58 (.78) | 23.80 (.45) | 23.38 (1.17) | 25.59 (.80) | 25.87 (.98) | 32.17 (.66) | 27.34 (1.10) | 31.37 (.71) | 32.13 (1.07) | 29.02 (1.05) | 24.32 (.43) | 28.89 (.86) |
| Mean Crown Area (m²/ha) | 2649.48 (201.46) | 1699.05 (106.92) | 789.10 (107.50) | 1712.54 (138.63) | 1247.23 (157.64) | 2387.95 (152.29) | 1686.84 (242.61) | 1845.84 (151.85) | 1188.08 (155.69) | 806.62 (125.69) | 974.17 (83.08) | 1448.10 (152.69) |

Table IV.2., Continued

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean Crown Volume (m³/plant | 5.00 (.47) | .98 (.11) | 1.07 (.15) | 2.27 (.23) | 2.07 (.28) | 3.49 (.45) | 6.02 (.30) | 2.82 (.17) | 5.26 (.29) | 2.82 (.14) | .32 (.03) | 3.26 (.24) |
| % Unburned | 100 | 100 | 100 | 100 | 14 | 1 | 0 | 0 | 2 | 3 | 4 | 3 |
| % Basal Sprouting | 0 | 0 | 0 | 0 | 47 | 3 | 0 | 5 | 12 | 29 | 58 | 22 |
| % Epicormic Sprouting | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0.6 |
| % Burned and Dead | 0 | 0 | 0 | 0 | 37 | 95 | 100 | 95 | 86 | 68 | 37 | 74 |

Three study sites were located in unburned *P. tridentata* stands. The predicted

age class distribution for the unburned sites was very similar to that of the burned sites.

Naturally occurring mortality in the absence of fire was evenly distributed across all age

classes, and averaged 5% (n=14) of all unburned shrubs sampled.

## Discussion

### Fire Ecology of *Purshia tridentata*

The 3 basic vegetation zones in which *P. tridentata* is present are typified by

historic short fire-return intervals. These include the dry conifer (usually *Pinus*

*ponderosa*), shrub-steppe, and juniper woodland zones (Bradley 1986). Within these

communities, historic fire-return intervals ranged from 5 to 50 years (Wright et al.

1979, Rice 1982). The regional age class structure of bitterbrush has shifted to older,

more decadent, and less resilient age classes.

Fire suppression has effectively disrupted the historic fire regime, which now

is resulting in greater levels of fire-induced mortality in *P. tridentata* communities

(Rice 1982). Early studies of fire effects on *P. tridentata* found that nearly any fire

event resulted in high rates of mortality, and therefore fire was perceived as a risk to

the valuable resource (Hormay 1943, Billings 1952). More recent reports have

identified *P. tridentata* as a facultative sprouter (i.e., having the capacity to

regenerate from sprouting or reproduce from seed) (Nord 1965). It has been

Table IV.3. List of predictive equations for estimation of *P. tridentata* age in the Hells Canyon, Idaho. Combinations of the following variables were tested in multiple regression modelling: shrub height (cm); crown area (m$^2$); and basal diameter (cm). SE given in parentheses.

| Equations | Standard Error of Model | Coefficient of Determination (R$^2$) |
|---|---|---|
| log(age) = 2.88 - .45*log(height) + 1.42*log(diam) - .05*log(C.Area) <br> (.66)  (.17)          (.20)                  (.11) | SE=0.36 | 0.69 |
| log(age) = 3.04 - .47*log(height) + 1.35*log(diam) * <br> (.57)  (.16)          (.14) | SE=0.35 | 0.70 |
| log(age) = 2.47 + .10*log(height) + .47*log(C.Area) <br> (.85)  (.19)          (.10) | SE=0.46 | 0.50 |
| log(age) = 1.23 + 1.17*log(diam) - .11*log(C.Area) <br> (.27)  (.18)          (.11) | SE=0.37 | 0.67 |

* Determined to be the best model for prediction of plant age and the formula utilized in this study

hypothesized (Driver 1982, Driver et. al. 1980, Martin and Driver 1982) that because *P. tridentata* persisted in ecosystems which evolved with a short fire-return interval, adaptations must exist to allow for regeneration or survival. Under a historic frequent-fire regime, it is likely that the majority of *P. tridentata* individuals were found in the younger age classes. Effective fire suppression within the study area has resulted in essentially no recruitment of the youngest age classes--the only segments of the population displaying an ability to sprout following fire.

Within the population sampled in this study, there was a significant decrease in the number of shrubs occupying the age classes > 40 years. Unburned shrubs in the oldest age classes were typified by decadence and notable amounts of dead foliage. Although *P. tridentata* has been noted to live as long as 160 years (Nord 1965), the oldest individuals sampled in this study were in the 55 to 60 year age class. There are many similar stands of bitterbrush across the western United States exhibiting decadence and stagnation in the absence of fire, which draws attention to the role of disturbance in the autecology of *P. tridentata* (Ferguson and Medin 1982). On a regional scale, dramatic differences are believed to exist in the density, age class distribution, and fire survival ability of *P. tridentata* between pre- and post-European settlement eras. These differences have been exacerbated by fire control policies which have left fire managers limited options to reintroduce fire into a once fire-dominated ecosystem.

## Fire Patterns and Age Class Partitioning of Burned Shrubs

Fire severity, as measured by the degree of fuel consumption observed, varied among the burned sites. Such variation was often due to differences in fuel loading and continuity. In addition, variation in climatic, topographic, and fuel-related factors in the fire environment (e.g., relative humidity, fuel moisture content, wind speed and direction) cause fire events in *P. tridentata* ecosystems to burn in a mosaic pattern (Bradley 1986).

Within burned plots, 3.5% (n=21) of all shrubs were not burned. In these plots, unburned individuals accounted for 0 to 14% of all shrubs. At the Snake River II plot, 50% (n=36) of all shrubs in the plot were completely consumed (only distinguishable by a root crown at the soil surface). In contrast, at the Ross Basin plot, 14% (n=11) of all shrubs were unburned. The unevenaged distribution of *P. tridentata* in this study may be attributable to such heterogeneity in previous burns. A mosaic pattern of burning would result in an unevenaged population structure; those individuals which were not burned would advance into older age classes while burned areas would recolonize with younger plants from sprouts or seedlings.

Within the study area, plant response was uniquely associated with each age class, revealing a correlation between plant age and fire survival ability (Table IV.4, Figure IV.1.). Driver et al. (1980) reported that in north-central Washington, the mean fire-return interval in a *Pinus ponderosa/Purshia tridentata* habitat type ranged between
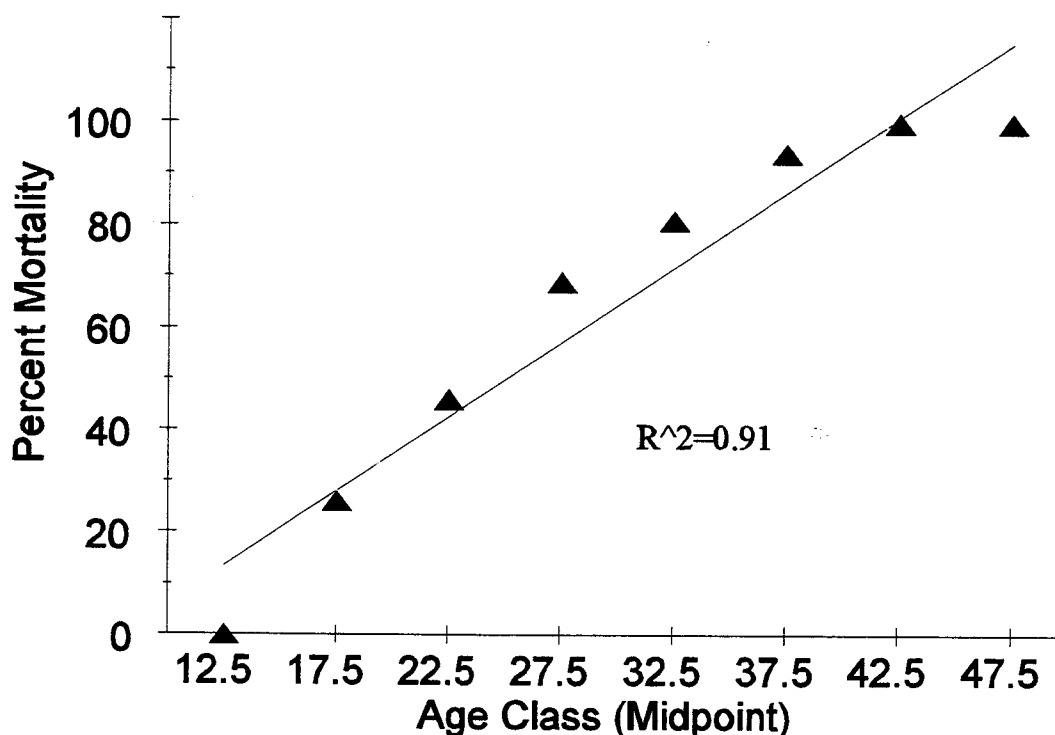
Figure IV.1. *Purshia tridentata* mortality (%) by age class (years) following the 1992 Windy Ridge Fire in the Hells Canyon, Idaho ($R^2=0.91$).

7 and 10 years. In this study, younger age classes retained their vigor and ability to

sprout following fire events, while post-fire mortality successively increased to 100% in

the oldest age classes. These findings suggest that in ecotypes of *P. tridentata* which

have a capacity to sprout, prescribed fire can be utilized to maintain younger and more

resilient age classes than those which would occur in the absence of fire. Applied on a

regional scale, reintroduced fire could theoretically minimize the extent to which *P.*

*tridentata* stands reach those stagnant and decadent conditions which have little, if any, capacity to sprout following fire.

The 25 year age class roughly corresponds to the longest fire-free interval which was typically experienced under a historic fire regime. Crane and Fischer (1986) reported that prior to 1900, the mean fire-return interval for habitat types including *P. tridentata* in west-central Idaho ranged from 5 to 25 years. Hence, it appears that ecological parallels exist between fire frequency, *P. tridentata* age class structure, and sprouting adaptations, and that effective fire suppression has rendered this relationship incongruent.

Considering the entire population sampled, *Purshia tridentata* assumed a bell-shaped distribution. The greatest recruitment occurred between 25 and 35 years ago, while there were only 2 shrubs out of 776 sampled which were predicted to be less than 10 years. There was not a short period of high recruitment resulting from a fire event, as is common for *Pinus contorta* Dougl. and *Salix scouleriana* Barratt. Rather, the *P. tridentata* communities sampled showed a distribution of cohorts with few individuals in the youngest age classes. Although this study suggests that a significant amount of regeneration from sprouting occurs in young *P. tridentata* stands following fire, it appears that regeneration continues for several years following the fire, presumably from seedling establishment.

Fire mosaics are characterized by unburned patches within the fire perimeter containing unburned individuals. One influence of unburned islands is in the succession

Table IV.4. *Purshia tridentata* survival and mortality by age class following the 1992 Windy Ridge Fire at the Payette National Forest, Idaho. Data are results of 491 shrubs from 7 stands sampled.

| AGE CLASS (Years) | % SPROUTING | % MORTALITY | SAMPLE SIZE (n) |
|---|---|---|---|
| 10-15 | 100 | 0 | 2 |
| 15-20 | 74 | 26 | 47 |
| 20-25 | 54 | 46 | 116 |
| 25-30 | 31 | 69 | 122 |
| 30-35 | 19 | 81 | 113 |
| 35-40 | 6 | 94 | 62 |
| 40-45 | 0 | 100 | 25 |
| 45-50 | 0 | 100 | 4 |

and repopulation of burned areas (Martin and Sapsis 1991). Perhaps an ecological

adaptation of *P. tridentata* is recolonization of the post-fire environment from unburned

sources. Equally likely is that when sprouting individuals reach reproductive maturity

(7-10 years), these then provide propagules for *P. tridentata* reestablishment (Nord

1965). Such a successional sequence would also result in an unevenaged population

structure.

## Ecological Implications of Altering a Fire Regime

A review of the literature and the age class distributions of the study area reveal

that the policy of fire suppression has greatly influenced the fire-free interval in these

communities. As a result, the historic fire regime has been altered and changes in community demography have followed. The majority of the *P. tridentata* populations sampled occupied age classes between 25 and 35 years (Table IV.4 and Figure IV.1). Only the youngest age classes (< 25 years) had high numbers of individuals that sprouted following fire. Hence, the historic population age class distribution has shifted to older age classes resulting in a diminished sprouting ability. Kauffman (1990a) reported that in certain species (e.g., *Quercus* spp.), fire adaptations such as sprouting may be altered during the life history of an individual. This study suggests that the ecological adaptation of basal sprouting in *P. tridentata* is greatly diminished as plant age exceeds 25 years.

Where frequent historic fire regimes have been lengthened, adverse responses in community composition have followed. In the grasslands of central Oregon and in the southwest deserts of the U.S.A., the reduction of fine fuels resulting from livestock grazing has led to a decrease in fire frequency. Associated with this temporal alteration are increases in western juniper (*Juniperus occidentalis* Hook) and honey mesquite (*Prosopis glandulosa* Torr.) and concomitant decreases in native grass communities and biological diversity (Kauffman 1990b).

Concomitant with changes in *P. tridentata* community structure have been compromises in the intrinsic fire responses of *P. tridentata* resulting from a lengthened fire-free interval, which was rarely if ever experienced in the historic disturbance regime. In the Lava Beds National Monument, California, an increase in the density of *P. tridentata* and *Cercocarpus ledifolius* Nutt. (curlleaf mountain mahogany) has resulted

in the absence of frequent fire (Johnson and Smothers 1976). In such habitats, fire-return intervals for *P. tridentata* communities may have been as frequent as 6 to 30 years, functioning to limit conifer and shrub density and maintain *P. tridentata* populations in younger age classes with an inherent capacity to sprout following fire (Arno 1976, Weaver 1957, Johnson and Smothers 1976).

In the study area, as well as other decadent stands across the western United States, this study suggests that *P. tridentata* communities have crossed an ecological threshold where there is a greatly diminished tendency to survive fires. Where fire once functioned to shift the age class distribution to the younger age classes, thereby maintaining stand structure and vigor, it will now kill the majority of the stand. However, in younger stands which have not reached decadence, in the study area being approximately 25 years of age, prescribed fire remains both a viable and necessary management practice to avoid this loss on a regional basis.

Prescribed fire represents an opportunity for the restoration of those *P. tridentata* stands which have not crossed an ecological threshold into decadence. If applied considering the key factors affecting post-fire survival (soil moisture, plant age, fire intensity, and season of burn), the management of bitterbrush can include fire to more closely resemble presettlement disturbance processes. These findings and others (Driver and Winston 1980) present the rationale why prescribed fire may be one avenue to mitigate against forfeiting the fire adaptation of basal sprouting, subsequent alterations in critical big game winter range, and the loss of *P. tridentata* on a regional scale.

## Conclusion

This study addressed the fire survivorship of *P. tridentata* in the Hells Canyon, Idaho. Utilizing a multiple regression model, we were able to predict the ages of 776 individuals by using plant height and mainstem basal diameter as predictive variables. The populations of 10 separate study sites were partitioned into age classes, and the fire survival within each age class was investigated.

Fire has played an important function in both the creation and maintenance of *P. tridentata* communities. Pre-settlement fire-return intervals were relatively frequent in ecosystems occupied by *P. tridentata*, with estimates ranging from 6 to 50 years between successive fires (Rice 1982). These low intensity fires resulted in a heterogeneous burn mosaic, sometimes killing the decadent segments of the population while stimulating sprouting in the younger age classes. This study suggests that the resulting age class distribution was skewed toward the younger ages, and that basal sprouting was the dominant fire adaptation facilitating the survival of the individual.

Effective fire suppression enacted in the past century has shifted the regional age class structure of *P. tridentata* to older age classes. The absence of younger age classes corresponds to inadequate post-fire recruitment, as this study indicates that the younger age classes are the only segment having the capacity to sprout. The age of 25 years appears to represent an ecological threshold for *P. tridentata* survivorship in the ecotype studied. Within the population sampled, plants < 25 years showed 66% sprouting, while plants > 25 years showed only 20% survival. The majority of the latter were from the

age class immediately proceeding 25 years. Additional factors which may have influenced the magnitude of survival via sprouting include soil moisture, degree of plant consumption, heat flux, and season of burn (Bradley 1986).

The paradox facing fire managers is how to best reintroduce fire, under a narrowing window of opportunity, in ecosystems were fire regimes have been disrupted, fire adaptations have been forfeited, and in certain cases, community structure has been altered. These difficulties are magnified by increasingly stringent social and environmental demands. Although the findings regarding patterns of mortality and survival are consistent with other general reports regarding *P. tridentata* fire response, these data should be considered specific to the study area. Extrapolation of the findings are subject to the variability noted among *P. tridentata* community parameters.

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**CHAPTER V**
**CONCLUSION**

Fire is one of many natural disturbance processes having profound influences on

ecosystem function, biogeochemical cycles, and diversity. The effects of fire can be

accurately described as variable both spatially and temporally. Within the Hells Canyon

environments, landscape mosaics reflect this variation in fire severity, periodicity, and

scale.

In subalpine forests of the Hells Canyon, community diversity and structure are

greatly influenced by fire (Johnson and Simon 1987). Circular relationships exist

between post-fire succession and recurring fires. Just as biotic assemblages are in large

part a manifestation of the fire regime, they in turn influence the scale and occurrence of

future fire events (Kauffman 1990a). A gradient of vegetation composition was detected

among the fire severity scenarios. Species diversity and richness were significantly

higher in partial stand-replacement forests than in complete stand-replacement or

unburned forests. Post-fire reestablishment in communities experiencing complete stand-

replacement was dominated by "invaders" (i.e., mobile, off-site immigrants) and

"evaders" (i.e., those establishing from arboreal or refractory seed pools). In contrast,

partial stand-replacement forests were dominated by a greater proportion of "endurers"

(i.e., species sprouting from taproots, rhizomes, or root crowns following top-kill) and

fewer "invaders". Dominants in unburned forests were characterized by "avoiders"--species capable of existing in late seral communities having essentially no adaptation to fire (Agee 1993, Stickney 1986).

Fire suppression has likely had little effect on such communities with infrequent (100 to > 300 year) fire return intervals (Crane and Fischer 1986). Because many fire events in these forests are associated with synoptic (i.e., hot, drought, and east wind) conditions, severe stand-replacement fires will continue to be a prominent element in the disturbance ecology of the Hells Canyon.

Possessing adaptive traits of both an "endurer" and an "invader", *Salix scouleriana* was an early seral dominant following severe, stand-replacement fires. Statistically significant changes occurred in mean shrub density, biomass ha$^{-1}$, and height from the fourth to the fifth post-fire year. Two distinct successional pathways were identified in willow-dominated communities. Where *Pinus contorta* was present in the pre-fire overstory, *Pinus contorta* saplings were present and advancing toward successional replacement of *Salix scouleriana*. Where *Pinus contorta* was absent in the pre-fire and post-fire environments, no trends away from *Salix scouleriana* dominance were detected. Based upon observations of post-fire succession in other areas of the Hells Canyon, this early seral community can persist for decades following fire.

*Purshia tridentata* is experiencing stagnation and high levels of post-fire mortality throughout the Pacific Northwest and Great Basin (Bradley 1986). Many ecotypes of this Rosaceous shrub valued for wildlife habitat, soil stability, and nutrient cycling have evolved in a fire-frequent environment which maintained younger age

classes having an inherent capacity to sprout follow fire (Tiedemann and Johnson 1983, Driver et al. 1980). Successful fire control policies have apparently shifted the age class distribution to older individuals most often killed by fire (Rice 1983). Following the 1992 Windy Ridge Fire, *Purshia tridentata* survival was inversely related to shrub age ($R^2$=0.91). Shrubs < 25 years of age exhibited 66% sprouting, while individuals > 25 years of age had 20% sprouting. Lengthened fire return intervals in *Purshia tridentata* stands place such communities at risk for high levels of post-fire mortality, associated with long-term alterations in range structure and associated wildlife habitats.

Despite an increasing knowledge base pertaining to disturbance ecology, implementing these findings will be difficult. Within the framework of natural resource management, land management agencies are directed to manage for a variety of often times mutually exclusive outcomes. Successful ecosystem management is complicated by the need to integrate science with social desires and attitudes in decision making. Because fire represents a central tool in ecosystem management, projecting desired future conditions of forests and rangelands requires consideration of the relevance of fire in community function and structure.

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# APPENDICES

Appendix A. Plant Species Codes, Common Names, and Latin Names of the flora of the Eagle Bar Fire.


## WOODY SPECIES:

| Sasc | Scouler willow | *Salix scouleriana* |
| Sage | Geyer willow | *Salix geyeriana* |
| Pico | Lodgepole pine | *Pinus contorta* |
| Abla | Subalpine fir | *Abies lasiocarpa* |
| Abgr | Grand fir | *Abies grandis* |
| Vagl | Globe huckleberry | *Vaccinium globulare* |
| Vame | thin-lvd. huckleberry | *Vaccinium membranaceum* |
| Vasc | grouse whortleberry | *Vaccinium scoparium* |
| Rila | prickly currant | *Ribes lacustre* |
| Rivi | sticky currant | *Ribes viscossissimum* |
| Rice | squaw currant | *Ribes cereum* |
| Spbe | shiny-leaf spirea | *Spirea betulifolia* |
| Sppy | pyramid spirea | *Spirea pyramidata* |
| Hodi | ocean-spray | *Holodiscus discolor* |
| Rupa | thimbleberry | *Rubus parviflorus* |
| Ceve | snowbrush | *Ceanothus velutinus* |
| Psme | Douglas-fir | *Pseudotsuga menziesii* |
| Rogy | little wild rose | *Rosa gymnocarpa* |
| Sosc | cascade mtn. ash | *Sorbus scopulina* |
| Amal | Pacific serviceberry | *Amalanchier alnifolia* |
| Phma | ninebark | *Physocarpus malvaceus* |
| Laox | western larch | *Larix occidentalis* |
| Sace | blue elderberry | *Sambucus cerulea* |
| Sara | black elderberry | *Sambucus racemosa* |
| Loin | black twinberry | *Lonicera involucrata* |
| Lout | Utah honeysuckle | *Lonicera utahensis* |
| Syal | common snowberry | *Symphoricarpus albus* |
| Acgl | Rocky Mtn. maple | *Acer glabrum* |
| Bere | creeping Oregon grape | *Berberis repens* |


## FORBS:

| Hyca | ballhead waterleaf | *Hydrophyllum capitatum* |
| Debi | little larkspur | *Delphinium bicolor* |
| Trlo | long-stalked clover | *Trifolium longipes* |
| Anmi | rosy pussytoes | *Antennaria microphylla* |

(Appendix A., Continued)

| Ergr | pale fawn lily | *Erythronium grandiflorum* |
| Cami | scarlet paintbrush | *Castilleja miniata* |
| Acmi | yarrow | *Achillea millefolium* |
| Lane | Nuttall's peavine | *Lathyrus nevadensis* |
| Epan | fireweed | *Epilobium angustifolium* |
| Epmi | small-flwd. willow-weed | *Epilobium minutum* |
| Eppa | tall annual willow-weed | *Epilobium paniculatum* |
| Clpu | deer horned clarkia | *Clarkia pulchella* |
| Lase | Chinese prickly lettuce | *Lactuca serriola* |
| Anpi | Piper's anemone | *Anemone piperi* |
| Vica | Canada violet | *Viola canadensis* |
| Cage | elk sedge | *Carex geyeri* |
| Popu | skunk-lvd. polemonium | *Polemonium pulcherrimum* |
| Povi | sticky polemonium | *Polemonium viscosum* |
| Soca | Canada goldenrod | *Solidago canadensis* |
| Luca | Kellogg's spurred lupine | *Lupinus caudatus* |
| Chum | Princes' pine | *Chimaphila umbellata* |
| Eqar | common horsetail | *Equisetum arvense* |
| Pyse | sidebells pyrola | *Pyrola secunda* |
| Mibr | Brewer's mitella | *Mitella breweri* |
| Giag | scarlet gilia | *Gilia aggregata* |
| Phlo | long-lf. phlox | *Phlox longifolia* |
| Caeu | big-pod Mariposa lilly | *Calochortus eurocarpus* |
| Ditr | Sierra fairy bell | *Disporum trachycarpum* |
| Smst | Star-fld. f. Sol. seal | *Smilacina stellata* |
| Smra | W. false Solomon's seal | *Smilacina racemosa* |
| Trov | wake robin | *Trillium ovatum* |
| Veca | false hellebore | *Veratrum californicum* |
| Zive | meadow death camas | *Zigadenus venonosus* |
| Ilri | streambank globemallow | *Iliamna rivularis* |
| Frve | woods strawberry | *Frageria vesca* |
| Arma | bigleaf sandwort | *Arenaria macrophylla* |
| Arco | heartleaf arnica | *Arnica cordifolia* |
| Gatr | sweet-scented bedstraw | *Galium triflorum* |
| Gaap | goosegrass bedstraw | *Galium aparine* |
| Hial1 | yellow hawkweed | *Hieracium albertinum* |
| Hial2 | wooly hawkweed | *Hieracium albiflorum* |
| Goob | rattlesnake plantain | *Goodyera oblongifolia* |
| Thoc | western meadowrue | *Thalictrum occidentalis* |
| Osch | sweet cicely | *Osmorhiza chilensis* |

(Appendix A. continued)

| | | |
|---|---|---|
| Vasi | mtn. heliotrope | *Valeriana sitchensis* |
| Urdi | stinging nettle | *Urtica dioica* |
| Veth | flannel mullein | *Verbascum thapsus* |
| Tofl | large-fld. tonella | *Tonella floribunda* |
| Pery | Rydberg's penstemon | *Penstemon rydbergii* |
| Copa | sm-fld. blue-eyed Mary | *Collinsia parviflora* |
| Hecy | roundleaf alumroot | *Heuchera cylindrica* |
| Trdu | yellow salsify | *Tragopogon dubius* |
| Phha | silverleaf phacelia | *Phacelia hastata* |
| Crin | common cryptantha | *Cryptantha intermedia* |
| Crto | Torrey's cryptantha | *Cryptantha torreyana* |
| Hafl | many flowered stickseed | *Hackelia floribunda* |
| Mepa | tall bluebells | *Mertensia paniculata* |
| Taof | common dandelion | *Taraxacum officinale* |
| Setr | arrow-leaved groundsel | *Senecio triangularis* |
| Sese | tall groundsel | *Senecio serra* |
| Sein | western groundsel | *Senecio integerrimus* |
| Ciar | Canada thistle | *Cirsium arvense* |
| Crac | tapertip hawksbeard | *Crepis accuminata* |
| Asal | alpine aster | *Aster alpiginus* |
| Asco | showy aster | *Aster conspicuous* |
| Asfo | leafy-bracted aster | *Aster foliaceous* |
| Aggl | false mtn. dandelion | *Agoseris glauca* |
| Anma | pearly everlasting | *Anaphilis margaritacea* |
| Gnmi | white cudweed | *Gnaphalium microcephalum* |
| Lodi | fernleaf desert parsley | *Lomatium dissectum* |
| Viam | American vetch | *Vicia americana* |
| Sial | Jim Hill tumble mustard | *Sisymbrium altissimum* |
| Aqfl | yellow columbine | *Aquilegia flavescens* |
| Aqfo | red columbine | *Aquilegia formosa* |
| Sior | Oregon campion | *Silene oregana* |
| Sido | Douglas campion | *Silene douglasii* |
| Sime | Menzie's silene | *Silene menziesii* |
| Chal | lambsquarter | *Chenopodium album* |
| Erhe | Parsley lvd. b.wheat | *Eriogonum heracleoides* |
| Mope | miner's lettuce | *Montia perfoliata* |
| Sela | lance-leaved sedum | *Sedum lanceolatum* |
| Jupa | Parry's rush | *Juncus parryi* |
| Agur | nettle-lvd. horse mint | *Agastache urticifolia* |
| Pogl | sticky cinquefoil | *Potentilla glandulosa* |

(Appendix A., Continued)

| Erci | crane's bill filaree | *Erodium cicutarium* |
|------|---------------------|---------------------|
| Podo | Douglas knotweed | *Polygonum douglasii* |
| Heun | Rocky Mtn. helianthella | *Helianthella uniflora* |
| Blsc | blepharipappus | *Blepharipappus scaber* |

## GRASSES:

| Dagl | orchard-grass | *Dactylis glomerata* |
|------|---------------|---------------------|
| Brvu | Columbia brome | *Bromus vulgaris* |
| Stoc | western needlegrass | *Stipa occidentalis* |
| Sihy | bottlebrush squirreltail | *Sitanion hystrix* |
| Caru | purple pinegrass | *Calamagrostis rubescens* |
| Elgl | blue wildrye | *Elymus glaucus* |
| Agex | spike bentgrass | *Agrostis exarata* |
| Agsp | bluebunch wheatgrass | *Agropyron spicatum* |
| Brca | mountain brome | *Bromus carinatus* |
| Brin | smooth brome | *Bromus inermis* |
| Dain | timber oatgrass | *Danthonia intermedia* |
| Kopy | prairie junegrass | *Koeleria pyramidata* |
| Mebu | oniongrass | *Melica bulbosa* |
| Phpr | common timothy | *Phleum pratense* |
| Pobu | bulbous bluegrass | *Poa bulbosa* |
| Popr | Kentucky bluegrass | *Poa pratensis* |
| Pose | Sandberg's bluegrass | *Poa secunda* |
| Trsp | spike trisetum | *Trisetum spicatum* |

Appendix B. Plant Species Codes, Common Names, and Latin Names
of the flora of the Windy Ridge Fire.


## WOODY SPECIES:

| | | |
|---|---|---|
| Abgr | Grand fir | *Abies grandis* |
| Acgl | Rocky Mtn. maple | *Acer glabrum* |
| Alin | mountain alder | *Alnus incana* |
| Amal | Pacific serviceberry | *Amalanchier alnifolia* |
| Arlu | wormwood | *Artemisia ludoviciana* |
| Arri | stiff sagebrush | *Artemisia rigida* |
| Artr | mountain big sagebrush | *Artemisia tridentata vas.* |
| Bere | creeping Or. grape | *Berberis repens* |
| Cere | hackberry | *Celtis reticulata* |
| Ceve | snowbrush | *Ceanothus velutinus* |
| Crdo | Douglas hawthorne | *Crataegus douglasii* |
| Hodi | ocean-spray | *Holodiscus discolor* |
| Phma | ninebark | *Physocarpus malvaceus* |
| Pipo | ponderosa pine | *Pinus ponderosa* |
| Potr1 | quaking aspen | *Populus tremuloides* |
| Potr2 | black cottonwood | *Populus trichocarpa* |
| Prem | bittercherry | *Prunus emarginata* |
| Prvi | chokecherry | *Prunus virginiana* |
| Psme | Douglas-fir | *Pseudotsuga menziesii* |
| Putr | antelope bitterbrush | *Purshia tridentata* |
| Rhgl | poison ivy | *Rhus glabra* |
| Rice | squaw currant | *Ribes cereum* |
| Rila | prickly currant | *Ribes lacustre* |
| Rivi | sticky currant | *Ribes viscossissimum* |
| Rogy | little wild rose | *Rosa gymnocarpa* |
| Rops | black locust | *Robinia pseudo-acacia* |
| Rupa | thimbleberry | *Rubus parviflorus* |
| Sace | blue elderberry | *Sambucus cerulea* |
| Sara | black elderberry | *Sambucus racemosa* |
| Sage | Geyer willow | *Salix geyeriana* |
| Sasc | Scouler willow | *Salix scouleriana* |
| Spbe | shiny-lf spirea | *Spirea betulifolia* |
| Sppy | pyramid spirea | *Spirea pyramidata* |
| Syal | common snowberry | *Symphoricarpus albus* |

(Appendix B., Continued)

FORBS:

| Acmi | yarrow | *Achillea millefolium* |
|------|--------|------------------------|
| Aggl | false mtn. dandelion | *Agoseris glauca* |
| Al | wild onion | *Allium spp.* |
| Amre | harvest fiddleneck | *Amsinckia retrorsa* |
| Anma | pearly everlasting | *Anaphilis margaritacea* |
| Anmi | rosy pussytoes | *Antennaria microphylla* |
| Aqfl | yellow columbine | *Aquilegia flavescens* |
| Aqfo | red columbine | *Aquilegia formosa* |
| Arco | heartleaf arnica | *Arnica cordifolia* |
| Asin | hairy milkvetch | *Astragalus inflexus* |
| Asle | freckled milkvetch | *Astragalus lentiginosus* |
| Basa | arrowleaf balsamroot | *Balsamorhiza sagittata* |
| Blsc | blepharipappus | *Blepharipappus scaber* |
| Caeu | big-pod Mariposa lilly | *Calochortus eurocarpus* |
| Cage | elk sedge | *Carex geyeri* |
| Cami | scarlet paintbrush | *Castilleja miniata* |
| Chal | lambsquarter | *Chenopodium album* |
| Chdo | hoary chaenactis | *Chaenactis douglasii* |
| Chum | Princes' pine | *Chimaphila umbellata* |
| Ciar | Canada thistle | *Cirsium arvense* |
| Ciin | wild chickory | *Cichorium intybus* |
| Clpu | deer horned clarkia | *Clarkia pulchella* |
| Coli | narrow-lvd. collomia | *Collomia linearis* |
| Copa | sm-fld. blue-eyed Mary | *Collinsia parviflora* |
| Crac | tapertip hawksbeard | *Crepis accuminata* |
| Crin | common cryptantha | *Cryptantha intermedia* |
| Crto | Torrey's cryptantha | *Cryptantha torreyana* |
| Debi | little larkspur | *Delphinium bicolor* |
| Drve | spring whitlow-grass | *Draba verna* |
| Epan | fireweed | *Epilobium angustifolium* |
| Eppa | tall annual w.-weed | *Epilobium paniculatum* |
| Eqar | common horsetail | *Equisetum arvense* |
| Erci | crane's bill filaree | *Erodium cicutarium* |
| Erhe | Parsley lvd. b.wheat | *Eriogonum heracleoides* |
| Erfl | yellow buckwheat | *Eriogonum flavum* |
| Ervi | broom buckwheat | *Eriogonum vimineum* |
| Erla | woolly sunflower | *Eriophyllum lanatum* |

(Appendix B., Continued)

| | | |
|---|---|---|
| Gaap | goosegrass bedstraw | *Galium aparine* |
| Gatr | sweet-scented bedstraw | *Galium triflorum* |
| Gevi | purple geranium | *Geranium viscosissimum* |
| Giag | scarlet gilia | *Gilia aggregata* |
| Gnmi | white cudweed | *Gnaphalium microcephalum* |
| Hial | yellow hawkweed | *Hieracium albertinum* |
| Hial | wooly hawkweed | *Hieracium albiflorum* |
| Hyca | ballhead w.leaf | *Hydrophyllum capitatum* |
| Jupa | Parry's rush | *Juncus parryi* |
| Lase | Chinese prickly lettuce | *Lactuca serriola* |
| Lida | Dalmatian toadflax | *Linnaria dalmatica* |
| Lodi | fernleaf desert parsley | *Lomatium dissectum* |
| Luca | Kellogg's spurred lupine | *Lupinus caudatus* |
| Medi | small-flowered mentzelia | *Mentzelia dispersa* |
| Mi | microseris | *Microseris* spp. |
| Mope | Miner's lettuce | *Montia perfoliata* |
| Onac | Scotch thistle | *Onopordum acanthium* |
| Pede | hot-rock penstemon | *Penstemon deustus* |
| Petr | whorled penstemon | *Penstemon triphyllus* |
| Peve | Blue Mt. penstemon | *Penstemon venustus* |
| Phha | silverleaf phacelia | *Phacelia hastata* |
| Phli | longleaf phacelia | *Phacelia linearis* |
| Phlo | long-lf. phlox | *Phlox longifolia* |
| Podo | Douglas knotweed | *Polygonum douglasii* |
| Pogr | slender cinquefoil | *Potentilla gracilis* |
| Pyse | sidebells pyrola | *Pyrola secunda* |
| Sasc | clear-eye | *Salvia sclarea* |
| Sein | western groundsel | *Senecio integerrimus* |
| Sela | lance-leaved sedum | *Sedum lanceolatum* |
| Sial | Jim Hill tumble mustard | *Sisymbrium altissimum* |
| Smst | Star-fld. f. Sol. seal | *Smilacina stellata* |
| Taof | common dandelion | *Taraxacum officinale* |
| Tofl | large-fld. tonella | *Tonella floribunda* |
| Trdu | yellow salsify | *Tragopogon dubius* |
| Trov | wake robin | *Trillium ovatum* |
| Urdi | stinging nettle | *Urtica dioica* |
| Vasi | mtn. heliotrope | *Valeriana sitchensis* |
| Veca | false hellebore | *Veratrum californicum* |
| Veth | flannel mullein | *Verbascum thapsus* |
| Viam | American vetch | *Vicia americana* |

(Appendix B., Continued)

Zive       meadow death camas       *Zigadenus venonosus*

## GRASSES:

| | | |
|---|---|---|
| Agin | intermediate wheatgrass | *Agropyron intermedium* |
| Agsp | bluebunch wheatgrass | *Agropyron spicatum* |
| Brbr | rattlesnake brome | *Bromus brizaeformis* |
| Brca | mountain brome | *Bromus carinatus* |
| Brin | smooth brome | *Bromus inermis* |
| Brja | Japanese brome | *Bromus japonicus* |
| Brmo | soft brome | *Bromus mollis* |
| Brte | downy brome | *Bromus tectorum* |
| Brvu | Columbia brome | *Bromus vulgaris* |
| Caru | purple pinegrass | *Calamagrostis rubescens* |
| Dagl | orchard-grass | *Dactylis glomerata* |
| Dain | timber oatgrass | *Danthonia intermedia* |
| Elci | basin wildrye | *Elymus cinereus* |
| Kopy | prairie junegrass | *Koeleria pyramidata* |
| Mebu | oniongrass | *Melica bulbosa* |
| Phpr | common timothy | *Phleum pratense* |
| Pobu | bulbous bluegrass | *Poa bulbosa* |
| Popr | Kentucky bluegrass | *Poa pratensis* |
| Pose | Sandberg's bluegrass | *Poa secunda* |
| Sihy | bottlebrush squirreltail | *Sitanion hystrix* |
| Stle | Letterman's needlegrass | *Stipa lettermannii* |
| Stoc | western needlegrass | *Stipa occidentalis* |