

AN ABSTRACT OF THE DISSERTATION OF

Kirk W. Davies for the degree of Doctor of Philosophy in Rangeland Ecology and Management presented on September 19, 2005.

Title: Community Analysis of the Wyoming Big Sagebrush Alliance and Functional Role of Wyoming Big Sagebrush

Abstract approved:

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This study consisted of two research projects in the Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance, the most extensive of the big sagebrush complex in the Intermountain West. In the first project, we intensively sampled 107 relatively undisturbed, late seral Wyoming big sagebrush sites across the High Desert, Humboldt, and western Snake River Ecological Provinces to investigate vegetation heterogeneity and the relationship of environmental factors with vegetation characteristics. Vegetation characteristics were highly variable across the region. Perennial grass and total herbaceous cover varied more than six and sevenfold, respectively between minimum and maximum values. Sagebrush cover averaged 12%, but ranged between 3 and 25%. With the exception of perennial grass cover ($p < 0.0001$, $r^2 = 0.52$), limited variability in other vegetation characteristics was explained by environmental variables.

In the second project, we investigated the functional role of Wyoming big sagebrush by using undisturbed and sagebrush removed (with burning) treatments and comparing vegetation and microsite characteristics under (subcanopy) to between sagebrush canopy (interspace) zones. Wyoming big sagebrush influenced associated vegetation and microsities. On sites receiving high incidental radiation, perennial grass and total herbaceous cover and density were greater in the subcanopy than interspace zones ($p < 0.05$). On north aspects, these differences were not as pronounced suggesting sagebrush's influence on associated vegetation is site dependent.

Temperature extremes were mediated and soil water content was greater in the subcanopy than interspace zones during the growing season. Results indicated that the subcanopy zone can be a more favorable environment to herbaceous vegetation than the interspace zone. Wyoming big sagebrush is important to community resource capture and use. Plots with sagebrush had greater soil water content at the start of the growing season and produced more total biomass compared to where sagebrush had been removed in both post-fire years ($p < 0.05$). However, higher Thurber's needlegrass photosynthetic rates and greater herbaceous cover and production where sagebrush had been removed suggested that more resources were available to herbaceous vegetation in the absence of sagebrush.

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Community Analysis of the Wyoming Big Sagebrush Alliance and Functional Role of
Wyoming Big Sagebrush

By
Kirk W. Davies

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APPROVED:

~~Redacted for Privacy~~

~~Co-Major Professor, representing Rangeland Ecology and Management~~

~~Redacted for Privacy~~

~~Co-Major Professor, representing Rangeland Ecology and Management~~

~~Redacted for Privacy~~

~~Head of the Department of Rangeland Ecology and Management~~

~~Redacted for Privacy~~

~~Dean of the Graduate School~~

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CONTRIBUTION OF AUTHORS

Dr. Jonathan D. Bates and Dr. Richard F. Miller were involved in the research design, data collection, and writing of the manuscripts.

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COMMUNITY ANALYSIS OF WYOMING BIG SAGEBRUSH ALLIANCE AND FUNCTIONAL ROLE OF WYOMING BIG SAGEBRUSH

CHAPTER 1

INTRODUCTION

Big sagebrush (*Artemisia tridentata* Nutt.)¹ comprises one of the major plant complexes in the western United States (Küchler 1970, Miller et al. 1994, West and Young 2000). The Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance is the most extensive of the big sagebrush complex (Miller and Eddleman 2000, Tisdale 1994). Wyoming big sagebrush communities are important for pastoral agriculture, wildlife habitat, carbon sequestration, biodiversity, and watershed function.

Since Euro-American settlement in the late 1800's Wyoming big sagebrush has decreased from its historic range. Following WWII, a large effort was made to reduce sagebrush to increase forage production for domestic livestock (Young et al. 1981). Conversion to agricultural cropland has eliminated Wyoming big sagebrush communities from extensive areas and contributed to the spread of non-native weeds. Currently, much of the Wyoming big sagebrush alliance is rated in poor condition and it is considered the least resilient and most susceptible alliance in the big sagebrush

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press. Seattle, WA. 730 p.

complex to invasion by exotic weeds (Miller and Eddleman 2000). Miller and Eddleman (2000) speculate that a majority of the exotic annual grasslands dominated by cheatgrass (*Bromus tectorum* L.) in the Intermountain West were formerly Wyoming big sagebrush communities. Presence of cheatgrass has increased fire frequency and size of fires resulting in replacement of native rangeland communities (Whisenant 1990). The conversion from native to exotic communities has resulted in a loss of wildlife habitat and rangeland productivity. Research and land management agencies have placed a major emphasis on developing strategies to maintain remaining intact landscapes and restoring degraded Wyoming big sagebrush communities. However, there is limited information describing 1) the heterogeneity of vegetation characteristics and 2) the influence of environmental factors on vegetation composition and structure in relatively undisturbed, late seral Wyoming big sagebrush communities. Furthermore, there is a limited understanding of the role of Wyoming big sagebrush in community dynamics.

The lack of information is of concern as management plans are developed and implemented. For example, recent disagreements have arisen over proposed guidelines and objectives for sage-grouse management because vegetation requirements were thought by rangeland ecologists to be beyond the potential of Wyoming big sagebrush communities at a stand, community, or landscape level. Thus, development of improved data bases are of critical importance to assist land

managers in protecting intact and restoring degraded Wyoming big sagebrush communities.

The purpose of this study was to measure the range of vegetation heterogeneity, the relationships between vegetation heterogeneity and environmental variables, and the influence Wyoming big sagebrush has at the microsite (under and between sagebrush canopies) and community level with fire as the driving disturbance mechanism. The objectives of the study include:

- 1) Determine the variability and range of vegetation characteristics of relatively undisturbed, late seral Wyoming big sagebrush sites in the northwest portion of the sagebrush biome.
- 2) Determine if distinct plant associations can be defined for this alliance.
- 3) Identify key environmental attributes correlated with plant species composition in this alliance.
- 4) Determine correlations between environmental variables and vegetation cover and structure in the Wyoming big sagebrush alliance.
- 5) Determine the microsite effect of sagebrush on microenvironment (air temperature, relative humidity, direct radiation) and soil characteristics (pH, texture, total carbon, total nitrogen, nitrogen available to plants, organic matter, and water content).
- 6) Determine the microsite effect of sagebrush on Thurber's needlegrass (*Stipa thurberiana* Piper) nitrogen isotope discrimination, nitrogen content, carbon isotope discrimination, photosynthetic rate, and stomatal conductance.
- 7) Determine the microsite effect of sagebrush on herbaceous production, cover, and density.
- 8) Determine the influence of sagebrush on community resource capture and use with fire as the driving disturbance mechanism.

CHAPTER 2

LITERATURE REVIEW

Sagebrush Ecology

Sagebrush (*Artemisia*)¹ plant communities occupy over 62 million hectares in the western United States (Küchler 1970, Miller et al. 1994, West and Young 2000). These communities extend across much of southern Idaho, eastern Oregon, Utah, Nevada, and western Montana down into western Colorado. Smaller populations are found in northern Arizona and New Mexico, northeastern California, eastern Washington, and southern British Columbia and Manitoba (McArthur and Plummer 1978, Tisdale et al. 1969).

The most widely distributed and abundant species of this genus is big sagebrush (*Artemisia tridentata* Nutt.) (Miller and Eddleman 2000). Big sagebrush is divided into three wide spread subspecies: basin big sagebrush (spp. *tridentata*), mountain big sagebrush (spp. *vaseyana* (Rydb.) Beetle), and Wyoming big sagebrush (spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) (Beetle and Young 1965). Two other big sagebrush subspecies are also recognized: xeric big sagebrush (spp. *xericensis* Winward ex R. Rosentreter & R. Kelsey), found on dry foothills in southern Idaho; and

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press. Seattle, WA. 730 p.

snowbank big sagebrush (spp. *spiciformis* (Osterhout) Kartesz & Gandhi), occupying high elevations in eastern Idaho, northern Utah, western Wyoming, and northwestern Colorado (Goodrich et al. 1985, McArthur 1983, Rosentreter and Kelsey 1991, Winward 1983).

Wyoming big sagebrush occupies xeric foothills and valleys with moderate to shallow soils at elevations of 700-2,150 m (Blaisdell et al. 1982, Hironaka 1978, McArthur and Plummer 1978, Morris et al. 1976, Tisdale 1994, Winward and Tisdale 1977). Tisdale (1994) stated that Wyoming big sagebrush is the most abundant and widely distributed subspecies of big sagebrush. Basin big sagebrush occupies valleys, plains, and foothills at elevations of 600-2,150 m in deeper, well drained, and more mesic soils than Wyoming big sagebrush (Barker and McKell 1983, Blaisdell et al. 1982, McArthur and Plummer 1978, Morris et al. 1976, Tisdale 1994, Winward and Tisdale 1977). Shumar and Anderson (1986) found that basin big sagebrush was more abundant on sandy soils than Wyoming big sagebrush, and the opposite was true on finer-textured soils, resulting in a gradient of distribution according to soil texture. When basin and Wyoming big sagebrush are found in adjacent populations, Wyoming big sagebrush occupies the warmer, drier, shallower, and less fertile soils (Barker and McKell 1983, Beetle and Young 1965, West et al. 1978). Mountain big sagebrush occupies foothills and mountain slopes of 1200-3000 m in elevation on deep, well-drained soils (Blaisdell et al. 1982, Tisdale 1994, Winward 1980). Mountain big sagebrush is generally found at higher elevations and in more mesic environments

than either Wyoming big sagebrush or basin big sagebrush. Beetle and Young (1965), Winward (1970), Hironaka et al. (1983) provide additional morphological and ecological differentiation among these three subspecies.

Sagebrush Community Classification

Sagebrush plant communities have been separated by dominant sagebrush species present encompassing relatively broad site and environmental characteristics (Blaisdell et al. 1982, Hironaka et al. 1983, Passey et al. 1982, Jensen et al. 1990). Further community subdivisions have differentiated major sagebrush species based on an array of understory indicator species, which have been quantified into Habitat Types by Hironaka et al. (1983), with soils into Cover Types by Jensen et al. (1990) and Ecological Sites (NRCS 1997, 2003).

The Habitat Type classification concept was first developed for forested vegetation (Daubenmire 1952) and was later adopted for shrubland systems (Poulton and Tisdale 1961, Hironaka et al. 1983). A Habitat Type is defined as an area that can support a particular climax plant community. The Habitat Type provides a basis for classifying plant communities into units, which are subject to similar environmental conditions. However, the broad inclusiveness of the Habitat Type in delineating plant communities results in a high degree of variability in associated soils. In many cases,

when the Habitat Type system was developed, detailed soil descriptions were lacking. Soils in the Habitat Type system have generally been described to the family level.

Differences among plant communities are well recognized, but there is little correlation among plant communities with a specific soil type. Because of their broad descriptive nature, Cover Types offer little detailed information of community structure, cover ranges, or interrelationships among vegetation-soil-environmental factors. Jensen et al. (1990) advised caution when Cover Types are used to infer a site's underlying soil properties. The assignment of Cover Types based on site and soil characteristics was proven to be highly inconsistent, particularly in more productive sagebrush communities (Jensen et al. 1990). This is because many diagnostic species used in the classification process possess wide ecological amplitudes and ecotypic variation (Passey et al., 1982, Doescher et al., 1985, West, 1988).

The Ecological Sites (Range Sites) concept was introduced by Dyksterhuis (1949) and has been extensively used by the Natural Resource Conservation Service (NRCS) and Bureau of Land Management (BLM) to classify rangelands into discrete units. Ecological Sites can be incorporated under Habitat Types as more discrete units detailing soil type, productive potential, major uses, and the associated potential natural plant community expected for the site (NRCS 1997, 2003). Ecological Site descriptions provide estimates of understory composition and productive response to annual precipitation (drought, average precipitation, above average precipitation), and

potential alternate stable vegetation states. A limitation of the Ecological Site classification, as inferred from research results (Jenson et al. 1990, Passey et al. 1982), is that potential natural communities can be found on a wide range of soil types.

None of the classification systems adequately describe vegetation characteristics important to wildlife. For many wildlife species, habitat requirements are often keyed to the structural characteristics of vegetation that provide cover as well as fulfilling nutritional demands.

Thus, weaknesses to the preceding classification systems and range site descriptions make it difficult to adequately ascertain the biological potentialities of the sagebrush ecosystem. Aside from Passey et al. (1982) there have been few studies differentiating structure and composition of relatively intact sagebrush communities both temporally and/or across environmental gradients in context with the soil resource. In most cases, vegetation measurements have not been adequate to provide a correlation with the soil resource. While studies have been successful at delineating the major sagebrush alliances, they have been less successful at separating out differences among plant associations within an alliance. Passey et al. (1982) and Jensen (1990) have come the closest to developing workable association groupings and associated soils characteristics for the major sagebrush species. Drawbacks to these studies were that they either 1) lacked replication to address the variability of vegetation and soils within a major alliance, as in the case of Passey et al. (1982); or 2) limited vegetation measurements to weight estimates, as in the case of Jensen et al.

(1990). In both studies the measurement of Wyoming big sagebrush sites was limited, Jensen et al. (1990) included only four and Passey et al. (1982) nine Wyoming sites in their analyses. Thus, there have not been intensive studies assessing biological potentials and variability within a single major sagebrush alliance, and this is particularly true for the Wyoming sagebrush alliance.

Wyoming Big Sagebrush Communities

Community Types and Productivity

The Wyoming big sagebrush alliance has been classified into communities by several authors covering various regions of the western United States (Passey et al. 1982, Hironaka et al. 1983, Shiflet 1994, NRCS 1997). Shiflet (1994) groups communities by the major sagebrush type but does not go into detail regarding cover, production, or composition in Wyoming big sagebrush communities. Hironaka et al. (1983) lists five Wyoming sagebrush Habitat Types for southern Idaho. The Habitat Type descriptions are very general in describing plant composition and structure but provide good descriptions of soils (family level), community response to disturbance, and management. Ecological Site descriptions for the Oregon High Desert Region include 14 Wyoming big sagebrush community types (NRCS 1997). Annual production on these sites ranges from 225 to 790 kg/ha on the dryer, shallow soil sites to 900 to 1350 kg/ha on more productive sites.

Passey et al. (1982) covered the largest geographic area (Wyoming, southern Idaho, northern Nevada, and northern Utah) and divided Wyoming big sagebrush alliance into 7 communities based on a productivity/environmental gradient.

Understory vegetation was characterized by the dominant perennial grasses including Thurber's needlegrass (*Stipa thurberiana* Piper), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), squirreltail (*Sitanion hystrix* (Nutt.) J.G. Sm.), native bluegrass (*Poa* L), and Idaho fescue (*Festuca idahoensis* Elmer). Productivity ranged between 550 and 885 kg/ha depending on site potential. Passey et al. (1982) grouped these communities into 3 categories: Dry End, Mesic, and Cold. Dry End sites (subgroups A & B) were dominated in the understory by squirreltail, lava aster (*Aster scopulorum* Gray), and western hawksbeard (*Crepis occidentalis* Nutt.).

Subgroup B has significantly greater productivity, higher cover (15% vs. 8%) and less bare ground (67% vs. 77%) than subgroup A. Both Dry End subgroups have more shrub cover than Mesic and Cold categories. The Mesic sites (Subgroups C, D, and E) are similar to each other but differ from other subgroups as a result of the presence of bitterbrush (*Purshia tridentata* (Pursh) DC.), Thurber's needlegrass, arrowleaf balsam root (*Balsamorhiza sagittata* (Pursh) Nutt.), and tapertip hawksbeard (*Crepis intermedia* Gray). Subgroup D has higher productivity and cover than E and C, and subgroup E has significantly more shrubs than the other two. Subgroup F differs from other groups in that Idaho fescue, prairie junegrass (*Koeleria cristata* auct. p.p. non Pers), and bitterbrush are prominent (Subgroup F is a single site and appears to

transition between Wyoming and basin big sagebrush). The cold category (Subgroup G) was a single site with presence of fringed sagebrush and was one of the least productive of the 7 subgroups.

None of the preceding classification systems provides adequate description of plant cover or structural aspects of the community (shrubs heights, visual obstruction, etc). Passey et al. (1982) cover estimates seem low but are close to what can be expected for the Wyoming big sagebrush type. NRCS (1997) estimates are confusing, with high covers in low productivity sites and lower cover in higher productive sites. Based on EOARC file data, the NRCS (1997) cover values tend to be grossly over-estimated.

Soils

Soils on Wyoming big sagebrush sites are typically a transition between Aridisols and Mollisols and usually possess a restrictive layer (bedrock, duripan, natric horizons). Common soil subgroups listed by Hironaka et al. (1983) include Xerollic Camborthids, Durixerollic Camborthids, Xerollic Durargids, and Aridic Haploxerolls. Soils described by Passey et al. (1982) are mostly intergrades among Xerollic Aridisols or Aridic Mollisols. Subgroups listed by Passey et al. (1982) are similar to Hironaka et al. (1983) but also include Lithic Haploxerolls - over fractured bedrock, and Argic Cyroborolls. NRCS (1997) provides the following subgroups for Wyoming big sagebrush communities in the Oregon High Desert: Xeric Argidurids, Typic

Argidurids, Aridic Durixerolls, Lithic Haploxerolls, Xeric Haplocambids, Lithic Argixerolls, Xerollic Haplocambids, Xerollic Haplargids, and Pachic Haploxerolls.

Community Variability

Wyoming big sagebrush community composition and structure are related to differences in site potential and condition. Differences in soil texture may influence dominant grass composition (Tisdale 1994). The amount and timing of precipitation as well as the ability of the site to retain the moisture, as determined by soil features, slope, aspect, and temperature, directly influences the potential level of production and amount of plant cover.

Within a Wyoming big sagebrush community, herbaceous productivity and cover varies with climatic conditions. Precipitation amounts and seasonality are highly related to site productivity (Blaisdell 1958, Sneva and Britton 1983, Bates 2004). Generally there is a positive relationship between total winter precipitation and production (Passey et al. 1982, Tisdale 1994, Bates 2004). Data from Passey et al. (1982) suggest that water in the soil at the beginning of the growing season can in part be used to explain annual fluctuations in productivity.

Variability in production is greater on the more productive sites, compared to sites with lower productive potential (Passey et al. 1982). Interannual production can vary by as much as tenfold, depending on weather factors (precipitation and temperature). The forb component is the most responsive to interannual climate variation (Passey et

al. 1982, Tisdale 1994, Bates 2004). Unless a major disturbance occurs, shrub cover is least responsive to interannual climate variation (Passey et al. 1982, Svejcar et al. 2003). Shrub cover in high seral Wyoming big sagebrush communities typically varies between 5 and 23% (Table 2.1.)

Table 2.1. Differences in shrub cover in Wyoming big sagebrush communities.

COMMUNITY	SHRUB COVER	LOCATION	REFERENCE
ARTRW8/FEID	7-25%	eastern Oregon	Doescher et al. 1986
ARTRW8/STCO2	0.3-22%	Utah	Goodrich et al. 1999
ARTRW8/AGSP	5.2-7%	Jordan Crater Kipukas	Kindschy 1992
ARTRW8/STTH	4-13%	EOARC Burns, OR	File Data
ARTRW8/FEID	5-22%	EOARC Burns	File Data
ARTRW8/AGSP	6.5% average	Mill, Utah	West and Hassan 1985

ARTRW8 = Wyoming big sagebrush, STCO2 = needle-and-thread grass (*Stipa comata* Trin. & Rupr.), AGSP = bluebunch wheatgrass, STTH = Thurber's needlegrass, and FEID = Idaho fescue.

Disturbance Effects

The ecological condition of Wyoming big sagebrush sites are the result of their disturbance history and resilience. Large areas of the Wyoming big sagebrush alliance in southern Idaho, Nevada, and Utah are in depleted condition due to improper grazing, past farming practices, and changes in fire regimes (Whisenant 1990, Tisdale 1994, Miller and Eddleman 2000).

Prior to the arrival of European settlers, fire was the main disturbance impacting the Wyoming big sagebrush alliance that shifted communities from shrub to perennial grass dominance. Fire-return intervals prior to European settlement have been estimated to vary between 50 and 100 years (Wright and Bailey 1982). Historic fires are also thought to have burned in a mosaic pattern creating a landscape of multiple-aged stands. Native vegetation often reestablished from unburned patches within the burn mosaic (Clifton 1981, Whisenant 1990).

Sites that have lost or have reduced native plant components due to improper grazing are more susceptible to invasion of exotics, particularly cheatgrass (*Bromus tectorum* L.). The loss of herbaceous components by heavy grazing pressure can also result in increased vigor, size, and density of woody shrubs (Winward 1991).

Cheatgrass has become a serious problem because understory dominance by this species may alter fire frequencies. In the Snake River Plains, cheatgrass dominance of the understory has resulted in increased fire frequency. Fire frequency in this area is now typically less than five years (Whisenant 1990). Dominance by a cheatgrass

understory over large areas may also create conditions promoting larger and more uniform fires than historical events (Whisenant 1990). More frequent and large uniform fires reduce the recovery potential of sites with a native component due to lack of protected unburned areas (Clifton 1981, Whisenant 1990). Under these conditions reestablishment of Wyoming big sagebrush communities becomes exceedingly difficult. Frequent fires may also reduce nutrients, further impeding reestablishment. Organic matter, nitrogen, and phosphorus can be volatilized and lost with burning (DeBano et al. 1979, DeBano 1989). Another potential difficulty with increased fire frequency is the removal or reduction of vesicular-arbuscular mycorrhizae associated with Wyoming big sagebrush communities (Gurr and Wicklow-Howard 1994). Mycorrhizae aids reestablishment of sagebrush by improving the sagebrush's ability to take up water (Stahl et al. 1998). These mycorrhizae may also promote reestablishment when phosphorus is limiting.

Wildlife Habitat Values of Wyoming Big Sagebrush

Sagebrush communities are recognized for their value as wildlife habitat. Many wildlife species are dependent on Wyoming big sagebrush communities for seasonal or year-round habitat. Fauna that are sagebrush obligates include sage-grouse, pronghorn antelope, pygmy rabbits, and a wide variety of migratory songbirds (Gregg et al. 1994, Yoakum 1986). Several species of big game and sage-grouse use

Wyoming big sagebrush areas for winter range. The Wyoming big sagebrush alliance provides excellent winter range because these areas are often warmer and more accessible than other big sagebrush alliances. Though sagebrush leaves possess protein levels similar to alfalfa (*Medicago sativa* L.), volatile oils and other compounds limit their consumption by big game. Palatability of sagebrush is variable, and big game use is probably influenced by availability of other browse and forage. Sheehy and Winward (1981) reported sagebrush was intermediately preferred by wintering mule deer and least preferred by domestic sheep. Bray et al. (1991) reported mule deer preferring Wyoming big sagebrush over basin and mountain big sagebrush. Sage-grouse and pronghorn often use the cover provided by Wyoming big sagebrush as rearing grounds (Gregg et al. 1994, Yoakum 1986).

Functional Role of Wyoming Big Sagebrush

Overview

Plant communities are directly and indirectly influenced by the presence of Wyoming big sagebrush. Wyoming big sagebrush's influence on community nutrient cycling and distribution has been described by Charley and West (1975) and Doescher et al. (1984). However, the influence of Wyoming big sagebrush on energy and water capture, evapotranspiration, microclimate, microtopography, soil characteristics, and herbaceous composition and structure heterogeneity are not well quantified. The

impacts of removing Wyoming big sagebrush with fire on community resource capture and use are also not well understood. Sagebrush's influence will likely vary by ecological site, condition of the site, and level of sagebrush dominance.

Resource Acquisition

Nutrients

The influence of sagebrush on soil nutrient and chemical distributions has been well documented in the literature. In Utah, higher concentrations of total nitrogen (N), organic carbon (C), and organic phosphorus (P) were found under big sagebrush plants (subcanopies) than in the shrub interspaces, but the reverse was true for total P (Charley and West 1975). Doescher et al. (1984) generally found higher concentrations of soil nutrients in the subcanopies than interspaces. In Wyoming big sagebrush/Thurber's needlegrass sites, they measured greater concentrations of total N, organic matter, and potassium (K) under sagebrush canopies in sites with a low proportion of grasses to shrubs. Sites with a high proportion of grasses to shrubs had higher concentrations of P and calcium (Ca) in the subcanopies than interspaces. They also found greater concentrations of various soil nutrients under big sagebrush canopies, compared to soils beneath grasses, depending on the subspecies of big sagebrush, associated dominant grass species, and proportion of perennial grasses to shrubs on the site. However, these differences diminished with increasing soil depth.

Ryel et al. (1996) measured increasing P and K with increasing proximity to a sagebrush base. They did not find any differences in ammonia (NH_4^+) or nitrate (NO_3^-) content between subcanopies and interspaces.

The concentration of nutrients beneath shrub canopies has been termed "islands of fertility" by some (West and Skujins 1977). Litter fall and root turnover under the canopies of shrubs and trees modifies soil chemistry (Fireman and Hayward 1952, Tiedemann and Klemmedson 1973, McDaniel and Graham 1992). Animals attracted to shrubs may also contribute to subcanopy nutrient loads (Vetaas 1992). Animals can be attracted to shrubs for various reasons including their ability to provide roosting sites, food, and hiding/thermal cover. Concentrations of animals around shrubs can increase fecal inputs and potentially carcasses deposition.

There are many examples of increased soil nutrients beneath arid land shrub canopies compared to interspaces. Plant communities where this has been reported include mesquite (Tiedemann and Klemmedson 1973), live-oak (Brejda 1998), creosote (Cross and Schlesinger 1999), and saltbrush (Bjerregaard 1971).

Soil Water

Besides the possibility of nutrient rich subcanopies improving associated vegetation growth, Richards and Caldwell (1987) suggested sagebrush might facilitate associated plants by increasing soil moisture in the sagebrush-rooting zone with hydraulic lift. Caldwell and Richards (1989) demonstrated there was a potential for this water to be used by associated tussock grasses.

Disturbance can potentially influence soil water availability in the sagebrush ecosystem. Soil water levels were generally lower in a highly degraded Wyoming big sagebrush site than an adjacent burned site (Murray 1975). However, these results are inconclusive because of lack of replication and differences between soils in the burned and unburned areas, which likely affected soil water-holding capacity and availability. The soil in the unburned area was classified as an Aridic Calcic Argixeroll, while the soil in the burned area was a Xerollic Natrargid. Sturges (1977a, 1983) measured changes in soil moisture depletion in sprayed and unsprayed mountain big sagebrush. Soil water depletion for the surface 0.9 m was slightly greater in sprayed than untreated mountain big sagebrush plots three years after treatment (Sturges 1983). Water depletion was significantly greater in the untreated plots between 0.9 and 1.8 m in the soil profile. However, because most soils in Wyoming big sagebrush communities are shallower than mountain big sagebrush, Sturges' research provides little insight into soil water depletion on Wyoming big sagebrush sites.

Structure and Micro-environment

Shrub architecture may modify the micro-environment by influencing capture of solar radiation (Pierson and Wight 1991), rainfall (Johnsen 1962), and windblown materials (West 1989). Interception will vary depending on size, shape, and density of canopies. Shading by shrub canopies in arid to semi-arid ecosystems reduces solar radiation and maximum daytime temperature near the ground surface (Johnsen 1962,

Tiedemann and Klemmedson 1977). Lower temperatures may increase soil water content through reduced evapotranspiration. Reduced temperature (and possibly shrub transpiration) may also increase relative humidity, thus reducing moisture stress on associated understory plants. Shading is also beneficial if excess light causes photoinhibition. Many plants experience some level of photoinhibition, especially in arid zones and at high latitudes and elevations (Powles 1984, Long et al. 1994, Horton et al. 1996). Excess shading, however, will also limit photosynthesis. In chaparral communities, large reductions of shrub cover were necessary to release white fir from overstory shrub competition, but the presence of a shrub canopy apparently increased survival of white fir (Conard and Radosevich 1982, Fowells and Schubert 1951). Tiedemann et al. (1971) reported four perennial southwestern grasses responded differently to shading. Though all species grew best in full sunlight, they varied in their ability to adapt to shade. Thus, the effect of shading depends on the level of shading and the understory species tolerance or adaptation to shading.

Sagebrush interception of rainfall may be minimal, because of its short stature and relatively open canopies. Johnsen (1962) found redistribution of moisture did not occur on one-seeded juniper trees (*Juniperus monosperma* (Engelm.) Sarg.) less than 2.5 ft tall. On larger one-seeded junipers, precipitation was intercepted and redistributed down the base of the plant. This resulted in soil moisture high near the base of the juniper, low around the canopy edge, and moderate in the interspace (Johnsen 1962). Studies of stem flow in western juniper (*Juniperus occidentalis*

Hook) have shown very small quantities of the intercepted rainfall actually flowing down the trunk (Young et al. 1984, Eddleman 1986). Precipitation intercepted by juniper canopies can be lost due to evaporation (Larsen 1993). The amount of through-fall precipitation depends on canopy structure and precipitation event characteristics.

Other authors have suggested that snow accumulations may be greater where sagebrush is present than absent. In areas of infrequent snow deposit, low drift potential, and periodic melting of accrued snow, accumulation of snow in sagebrush communities is less likely (Murray 1975). However, where snowfall does occur, snowdrift accumulation on sites containing big sagebrush would be more likely than sites where sagebrush is absent. In Wyoming, Hutchison (1965) found significantly more snow accumulation on sagebrush sites than adjacent grasslands, because sagebrush intercepted drifting snow. Sturges (1977b) initially measured similar differences between an undisturbed and sprayed mountain sagebrush community, but once snow covered the sagebrush in the undisturbed community there was no difference in total snow accumulation or rate of snow melt among treatments.

Litter may improve infiltration by modifying physical properties of the soil surface, ameliorating temperature, and reducing evaporation (Tiedemann and Klemmedson 1977, Tiedemann and Klemmedson 1973). Evans and Young (1970) found litter moderated moisture and temperature, thus creating a microsite favorable to germination of weedy annual grasses. Contrary to these studies, Larsen (1993)

suggested litter interception of precipitation may increase loss via evaporation. Interception losses from juniper litter can be higher than losses from interception by the tree canopy (Larsen 1993). He suggested that this might create areas beneath juniper trees where precipitation rarely reaches the mineral surface. Different litter depths and physical and chemical properties probably explain these discrepancies.

Texture of the soil beneath shrubs may differ from interspace areas, due to capture of windblown soil particles. In shrub live-oak communities, Brejda (1998) reported finer soil texture beneath than between shrub canopies.

Competition and Facilitation

The effects from sagebrush resource acquisition and sagebrush's structure on associated plant species growth can be positive (facilitative) and/or negative (competitive). Competition and facilitation between sagebrush and associated species are probably occurring simultaneously on the sagebrush steppe. This relationship may vary by season, site, abundance of sagebrush, and site condition.

Nitrogen and phosphorus are often the nutrients most limiting to plant growth in arid to semi-arid regions (West and Skujins 1978). Plants growing under the canopies of sagebrush may benefit from greater nutrient availability or suffer from greater competition or interference. Charley and West (1977) suggest that enhanced nitrogen availability would increase water-use efficiency of understory species. The availability of resources under the sagebrush canopy to associated vegetation has not

been determined. However, competition in the interspace for phosphorus (P) between sagebrush and perennial bunchgrasses has been demonstrated by Caldwell et al. (1987, 1991). Sagebrush was able to acquire about six times more P than bluebunch wheatgrass (Caldwell 1991).

Species establishment and growth can differ depending on proximity to sagebrush canopies. Callaway et al. (1996) found survival of singleleaf pinyon (*Pinus monophylla* Torr. & Frém.) seedlings were higher under big sagebrush canopies than between them, while the opposite was true for ponderosa pine (*Pinus ponderosa* P.& C. Lawson). Chambers (2001) also found survival of singleleaf pinyon was greater under big sagebrush canopies. Miller and Rose (1995) measured faster growth rates of young western juniper growing beneath mountain big sagebrush than in the interspaces. These varying responses suggest the balance between competition and facilitation may be species dependent in the sagebrush steppe ecosystem.

Fire Disturbance

Historical and Current Fire Regimes

Fire regimes have been drastically altered across the Wyoming big sagebrush alliance, with some regions experiencing more frequent and spatially complete fires. Prior to European settlement, fire-return intervals are thought to have varied between 50 and 100 years in the Wyoming big sagebrush alliance (Wright and Bailey 1982).

Fire was a natural disturbance within this alliance that shifted communities from shrub dominance to grass dominance (Wright and Bailey 1982). Presently large areas of Nevada and Idaho's Snake River Plains are experiencing fire frequencies of less than five years because of cheatgrass dominance in the understory (Whisenant 1990). Dominance by a cheatgrass understory over large areas may also create conditions promoting larger and more uniform fires than historical events (Whisenant 1990). These conditions perpetuate the continued existence of the exotic annual communities at the expense of native communities. Shortened fire-return intervals will probably not allow for reestablishment of Wyoming big sagebrush communities.

Effects of Fire on Soil

Burning affects chemical and physical characteristics of soils. The degree of alteration appears to vary by fire intensity and vegetation type.

Chemical differences between burned and unburned sagebrush soils appear to be limited to the upper soil horizons. Blank and Young (1989) reported chemical differences were largely confined to the upper 5 cm of the soil. Soil nutrients may be lost as a result of fire. DeBano (1989) measured substantial losses of N and P by volatilization with chaparral burning, though extractable ammonium and P were increased by ash fall (DeBano et al. 1979). The amount of nutrients lost is positively correlated with increased burn temperatures (DeBano 1989).

Physical changes are often due to the loss of organic matter through vaporization. Organic matter bonds soil particles together and thus is important to soil structure. Most surface organic matter is volatilized and lost. However, small amounts of organic matter move downward in the soil, causing water-repellent layers to form (DeBano et al. 1979). Water-repellent soil can form when leaf mulch under a sagebrush burns, though the cooler the burn the less likely this will occur (Salih et al. 1973). Pierson et al. (2001) found that former subcanopies were more water-repellent and erosion prone the year after burning than interspaces.

Microtopography is a surface physical attribute of the soil which is often overlooked when considering changes to the soil. In the sagebrush steppe, microtopography may be increased by the presence of subcanopies and interspaces. Microtopography is important in preventing soil erosion (Eltz and Norton 1997) and retaining nutrients on site (Dunne et al. 1991). Changes in microtopography could have profound implications on soils and sequentially the vegetation.

Effects of Fire on Vegetation

Within the sagebrush community, species responses to fire vary. Perennial grass response to burning appears to be dependent on plant size, density of crown fuels, seasonality of burn, and burn intensity. Idaho fescue often suffers long-term damage following fire (Blaisdell 1953, Hironaka et al. 1983). Needle-and-thread and Thurber needlegrass also respond negatively to fire (Uresk et al. 1976, Wright 1971, Wright

and Klemmedson 1965). Young and Miller (1985) and Vose and White (1991) found squirreltail to respond positively to burning, while Wright and Klemmedson (1965) found squirreltail to be unaffected by burning. Wright and Klemmedson (1956) also found Sandberg bluegrass (*Poa sandbergii* Vasey) to be unaffected by burning. Bluebunch wheatgrass frequency and basal area may remain unchanged (Peek et al. 1979), or its production may increase over the short term after fire (Blaisdell 1953 and Uresk et al. 1976).

Response of herbaceous biomass production following fire varies. Harniss and Murray (1973) reported an initial decline in herbaceous production the first post-burning year, followed by an increase to above pre-burn production by the second post-burning year, while Uresk et al. (1976) found production increased in the first post-burn season.

Forb response to burning is dependent on individual species adaptations to fire, seed bank, and pre- and post-burn climatic conditions. Pyle and Crawford (1996) found prescribed burning had no effect on microsteris (*Microsteris gracilis* (Hook.) Greene), while Humphrey (1984) found its cover to be significantly higher following fire than in later successional stages. Pyle and Crawford (1996) suggested the discrepancy could be due to burning in the spring during germination and with a drought following their burn.

Shrub recovery immediately after fire is dependent on resprout ability and/or seed banks characteristics. Big sagebrush does not resprout (Beetle and Young 1965) and

therefore is easily killed by burning. Rabbitbrush (*Chrysothamnus* sp Nutt.) resprouts (Akinsoji 1988) and often increases in density and size after burning (Kunzler et al. 1981). Germination and establishment of Wyoming big sagebrush is sporadic (Maier et al. 2001). Often many years pass before conditions promoting successful germination and establishment of sagebrush occur (Maier et al. 2001).

CHAPTER 3

**VEGETATION CHARACTERISTICS OF THE WYOMING BIG
SAGEBRUSH ALLIANCE ACROSS PART OF ITS NORTHWESTERN
RANGE**

Kirk W. Davies, Jonathan D. Bates, and Richard F. Miller

VEGETATION CHARACTERISTICS OF THE WYOMING BIG SAGEBRUSH ALLIANCE ACROSS PART OF ITS NORTHWESTERN RANGE

Abstract

The Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance is the most extensive of the big sagebrush complex in the Intermountain West. This alliance provides critical habitat for many sagebrush obligate and facultative wildlife species as well as a forage base for livestock production. However, there is a lack of information describing vegetation cover potentials and heterogeneity across the Wyoming big sagebrush alliance. This study describes the cover potentials and spatial heterogeneity of late seral Wyoming big sagebrush plant associations across part of the northwestern portion of the sagebrush biome. Our objectives were to: 1) describe vegetation characteristics in relatively undisturbed Wyoming big sagebrush plant communities; and 2) determine if distinct plant associations could be defined. We intensively sampled 107 relatively intact, late seral Wyoming big sagebrush sites. We found total herbaceous cover values could vary more than sevenfold among sites. Perennial forb, sagebrush, Sandberg bluegrass, annual forb, and annual grass cover values were more variable than total herbaceous cover. Variation was reduced by forming associations. We separated this alliance into five associations by dominant perennial bunchgrass species. Differences in vegetation characteristics support using perennial bunchgrass species to separate the Wyoming

big sagebrush alliance into associations. Vegetation requirements from sage-grouse management guidelines were generally beyond the potential of the Wyoming big sagebrush sites sampled; thus, demonstrating that the vegetation requirements from sage-grouse management guidelines should not be used as management standards for the Wyoming big sagebrush alliance.

Introduction

Big sagebrush (*Artemisia tridentata*)¹ comprises one of the major plant complexes in the western United States (Küchler 1970, Miller et al. 1994, West and Young 2000). The Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance is the most extensive of the big sagebrush complex in the Intermountain West (Miller and Eddleman 2000, Tisdale 1994). Wyoming big sagebrush communities are important for pastoral agriculture, wildlife habitat, and biodiversity.

Since Euro-American settlement in the late 1800's the Wyoming big sagebrush alliance has decreased from its historic range. Following WWII, a large effort was made to reduce sagebrush to increase forage for domestic livestock (Young et al. 1981). Conversion to agriculture cropland has also eliminated Wyoming big sagebrush communities from extensive areas and contributed to the spread of non-

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. *Flora of the Pacific Northwest*. University of Washington Press. Seattle, WA. 730 p.

native weeds. Miller and Eddleman (2000) speculate that a majority of the exotic annual grasslands dominated by cheatgrass (*Bromus tectorum* L.) in the Intermountain West were formerly Wyoming big sagebrush communities.

Research and land management agencies have placed a major emphasis on developing strategies to maintain remaining intact landscapes and restoring degraded Wyoming big sagebrush communities. However, there is limited information describing the basic vegetation characteristics and potentials of the Wyoming big sagebrush alliance in relatively undisturbed, late seral condition. Anderson and Inouye (2001) described vegetation characteristics on 47 Wyoming big sagebrush plots that had been undisturbed for 45 years, but their study was limited to the Idaho National Engineering and Environmental Laboratory in southeastern Idaho. Passey et al. (1982), Tisdale and Hironaka (1981), Kindschy (1992), and Jensen (1990) in their efforts provide some details of this alliance, but their studies suffer from small sample size and/or limited characterization of vegetation cover.

The lack of information is of serious concern as management plans are developed and implemented. For example, recent disagreement has arisen over vegetation requirements in sage-grouse management guidelines developed by Connelly et al. (2000) and Bureau of Land Management (BLM) et al. (2000) (Appendix 1). Vegetation requirements in the guidelines were developed from small scale habitat studies, however, these vegetation requirements are being interpreted as applicable at

the stand, community, and landscape scales¹. Many rangeland ecologist and federal land managers doubt that these vegetation requirements can be achieved in Wyoming big sagebrush communities when applied at the stand, community or landscape scale. The lack of adequate descriptions of vegetation characteristics in relatively undisturbed, late seral sagebrush communities makes it difficult to recommend adjustments to current vegetation requirements in sage-grouse guidelines and to develop useful management criteria that will assist land managers in protecting intact and restoring degraded sagebrush communities. Management objectives also need to be tailored to the individual subspecies of the big sagebrush complex because of differing environmental characteristics influencing vegetation structure and composition and varying responses to grazing and disturbance (Barker and McKell 1983, Beetle and Young 1965, Blaisdell et al. 1982, Hironaka 1978, McArthur and Plummer 1978, Morris et al. 1976, Tisdale 1994, Winward and Tisdale 1977).

The objectives of this study were to 1) determine the variability and range of vegetation characteristics of relatively undisturbed, late seral Wyoming big sagebrush sites in the northwest portion of the sagebrush biome; and 2) determine if distinct plant associations could be defined for this alliance.

¹ **Landscape** – a heterogeneous land area composed of many plant communities.
Plant community – an assemblage of species across an area with one dominant overstory species.

Stand – a continuous, relatively homogenous area with one dominant overstory species and one or two dominant understory species.

Methods and Statistics

Site Selection

In February, March, and April of 2001 and 2002, Bureau of Land Management (BLM) offices in Lakeview, Vale, Burns, and Winnemucca were contacted to obtain locations of Wyoming big sagebrush communities in high ecological, late seral condition in the High Desert, Humboldt, and Snake River ecological provinces. The BLM wildlife and rangeland experts in addition to ecological site inventory maps were used to focus our initial search for relatively intact, late seral Wyoming big sagebrush sites. Every relatively intact, late seral site found was sampled. Sites were selected using the following criteria: 1) the understory was dominated by large native perennial bunchgrasses and native forbs, 2) exotic species were a minor to nonexistent component, 3) there was evidence of limited livestock use based on criteria developed by Passey et al. (1982), and 4) stands were dominated by a mature stand of Wyoming big sagebrush with limited recruitment of new shrubs (no recorded fire at sites for > 50 years). At each selected site a complete soil description was performed to determine the Ecological Site. Vegetation measurements were compared to the Ecological Site Descriptions to ensure sites were late seral. All sites included in our analysis met stricter requirements than those used for reference sites in rangeland health assessments (Pellant et al. 2005). We sampled 107 sites that met these criteria.

Most sites were in the High Desert and Humboldt ecological provinces with a few located in the western edge of the Snake River ecological province (Fig. 3.1). Sites were located in sage-grouse habitat: 78 sites in year-round occupied habitat and 29 sites in occupied, seasonal use uncertain habitat, 30 sites were within 2 km of a lek, 66 sites were within 5 km of a lek, and 99 sites were within 10 km of a lek (BLM-Burns database). Sites were sampled from late May to the first of July to capture peak vegetation cover. When feasible, we sampled in areas with an array of different site characteristics (e.g. slope, elevation, aspect, soil, and dominant grass species) to quantify variation across the Wyoming big sagebrush alliance and within plant associations.

Sampling

One randomly located 80 X 50 m (0.4 ha) plot was used to sample each site (Appendix 2). Five 50 m transects spaced at 20 m intervals were deployed along the 80 m transect. Shrub canopy cover by species was measured by line intercept (Canfield 1941) and separated into live and dead components. Canopy gaps greater than 15 cm were excluded from canopy cover measurements. Herbaceous canopy cover was visually estimated by species inside 40 x 50 cm (0.2 m²) frames located at 3 m intervals on each transect line (starting at 3 m and ending at 45 m), resulting in 15 frames per transect and 75 frames per plot. Fifty randomly selected sagebrush heights were measured in each plot. A species list was compiled for each 0.4 ha plot.

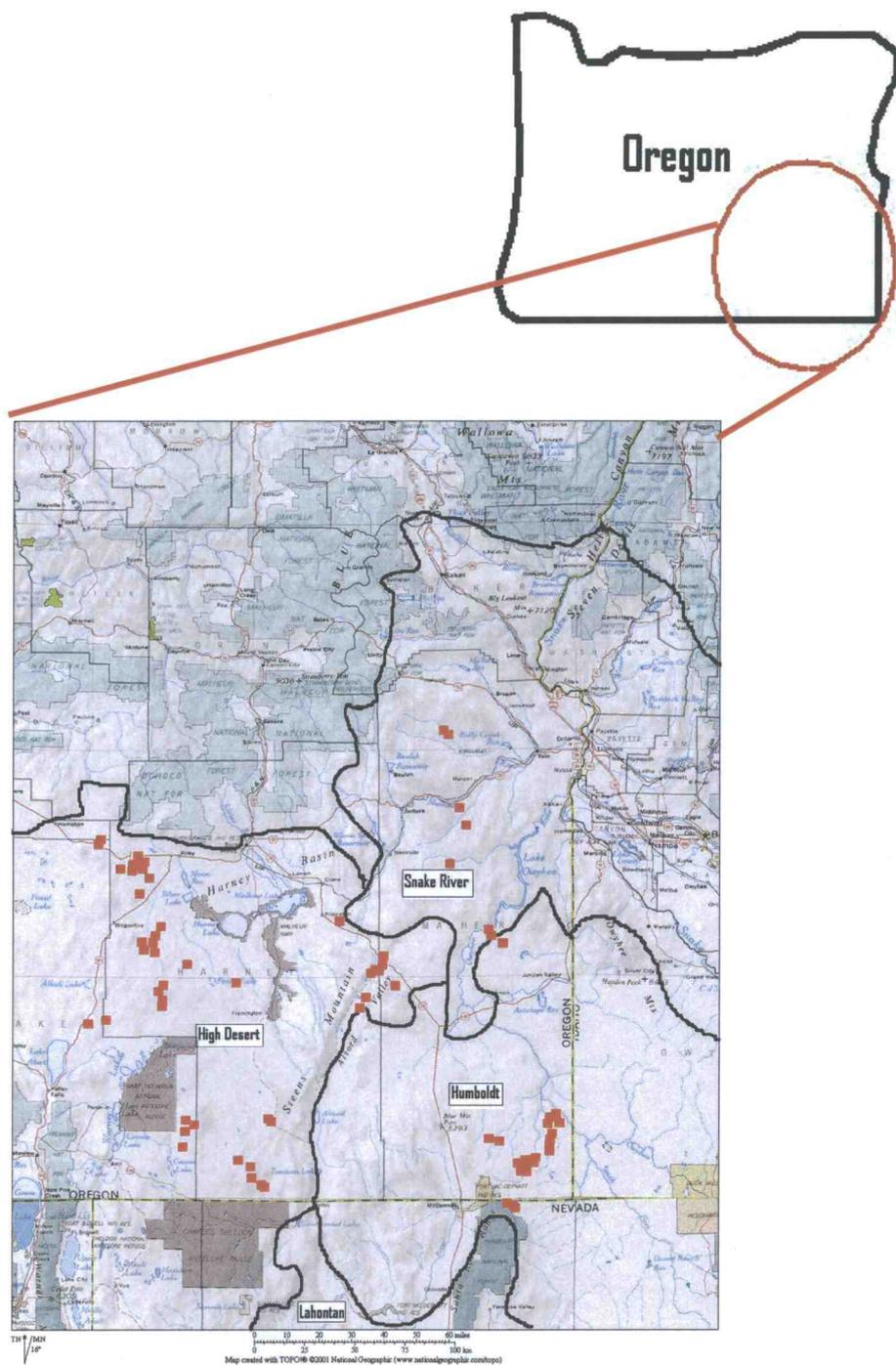


Figure 3.1. Study site locations. Red squares represent areas where Wyoming big sagebrush sites were sampled. Ecological province boundaries (bold black lines) are derived from Anderson et al. (1998) and Bailey (1994).

Statistical Analysis

Descriptive statistics (means, minimums, maximums, standard errors, and other parametric statistics) (S-plus 2000) were generated to summarize vegetation characteristics of the Wyoming big sagebrush sites sampled. For summaries, herbaceous cover was grouped into five functional groups: Sandberg bluegrass (POSA), tall tussock perennial grass (PG), annual grass (AG), perennial forbs (PF), and annual forbs (AF). Functional groups simplify analysis and allow comparisons among sites with different species compositions. The purpose of using functional groups is to combine species that respond similarly to environmental perturbation and to reduce data to a simpler form for analysis and presentation (Boyd and Bidwell 2002). Cluster analysis and personal judgment were used to group sites (according to their dominant perennial bunchgrass composition) into distinct plant associations. Once associations were formed, parametric statistics were used to summarize the vegetation characteristics of each association. A Multiple Response Permutation Procedure (MRPP) was used to test for species composition homogeneity within associations (PC-ORD version 4). In a MRPP, the A statistic is the chance-correct within-group agreement (McCune and Grace 2002). If A is > 0 , then there is more homogeneity than expected by chance within groups. If all individuals within a group are identical then $A = 1$. If there is less agreement within groups than expected by chance, then $A < 0$. Analysis of variance (ANOVA) was used to determine if

differences in vegetation cover existed among associations and family-wise comparisons using the Tukey-Kramer method were used to determine which associations were different from each other (S-plus 2000). Vegetation cover and height characteristics were compared to Bureau of Land Management et al. (2000) and Connelly et al. (2000) sage-grouse habitat requirements. Tall forb cover (> 18 cm) was liberally estimated by including the cover of all forb species that had been observed to reach 18 cm in height on late seral Wyoming big sagebrush sites. Tall grass cover (> 18 cm) was liberally estimated to include all perennial grass cover.

Results and Discussion

Summary of Vegetation Characteristics

Herbaceous cover

Herbaceous vegetation cover was highly variable across the 107 sites sampled (Table 3.1). Tall tussock perennial grass and total herbaceous cover varied more than six and sevenfold between minimum and maximum values, respectively. Tall tussock perennial bunchgrasses accounted for 53% of the total herbaceous cover across all sites sampled. Annual grass cover was low to nonexistent on most sites sampled. Perennial forb cover accounted for less than 20% of the total herbaceous cover across the sites. Tall (>18 cm) forb cover averaged 1.9% with a standard error of 0.196%

(Fig 3.2). The functional group cover values we measured were within the range of covers reported by Anderson and Inouye (2001) and Kindschy (1992). Anderson and Inouye (2001) reported 0.13% Sandberg bluegrass, 5.5% perennial grass, and 2.85% perennial forb average cover values for 47 Wyoming big sagebrush plots in southeastern Idaho that had not been grazed or otherwise disturbed for 45 years. In southeastern Oregon, Kindschy (1992) reported a Wyoming big sagebrush community in a kipuka (surrounded by lava) with 5.2% sagebrush, 3.6% Sandberg bluegrass, 7.6% perennial forb, and 24.6% perennial grass cover.

Table 3.1. Variability of functional group percent canopy cover values across all sites measured.

STATISTIC	POSA (%)	PG (%)	AG (%)	PF (%)	AF (%)	Total herb (%)
Mean	5.39	12.19	0.61	4.13	0.59	22.91
Median	5.28	10.85	0.05	3.61	0.37	21.92
Min	0.0	4.5	0.0	0.0	0.02	5.9
Max	13.21	28.3	9.8	11.9	5.6	46.5
Standard Error	0.23	0.45	0.14	0.27	0.07	0.66

POSA= Sandberg bluegrass, PG = Tall tussock perennial grass, AG = Annual grass, PF = Perennial forb, AF = Annual forb, and Total herb = Total herbaceous

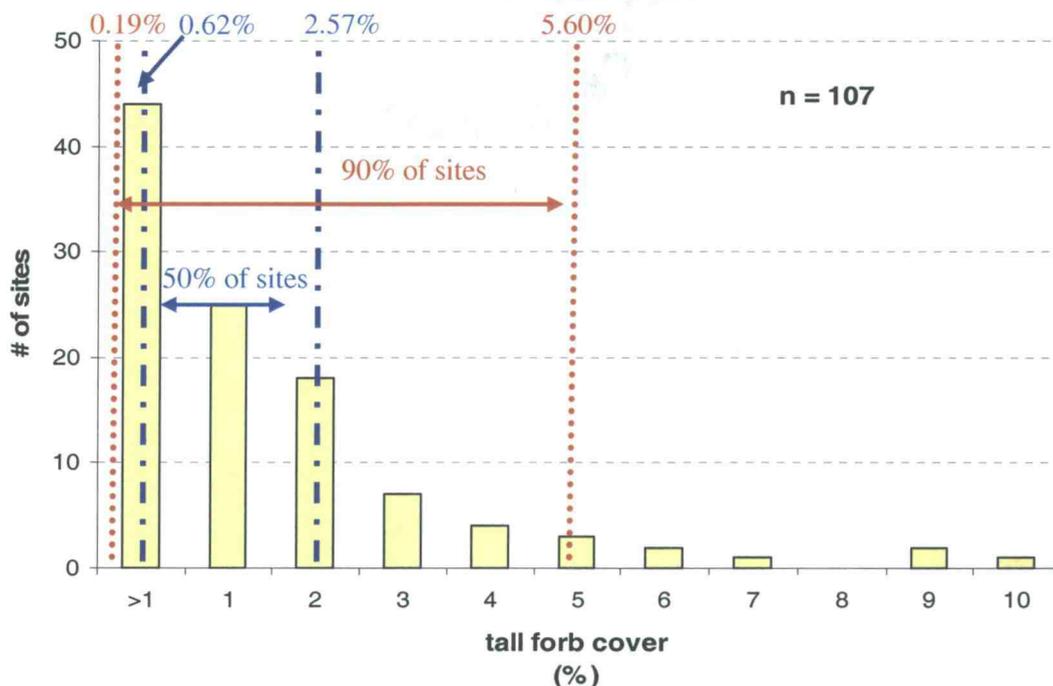


Figure 3.2. The number of sites that produced certain quantities of tall forb cover. The x-axis labels are percentage categories.

Shrub cover

Shrub canopy cover was also highly variable across the sites sampled (Table 3.2). The majority of sites had sagebrush canopy cover between 6 and 20% (Fig. 3.3). Wyoming big sagebrush canopy cover values from our sites were similar to values reported by Doescher et al. (1986), Goodrich et al. (1999), Kindschy (1992), and West and Hassan (1985) (Table 3.3)

Table 3.2. Summary of shrub percent canopy cover values for all sites measured.

STATISTIC	Live Sagebrush (%)	Dead Sagebrush (%)	Other Shrub (%)	Total Live ^a (%)	All Shrub ^b (%)
Mean	12.3	3.9	1.1	13.4	17.3
Median	11.9	3.5	0.4	12.3	17.0
Min	3.2	0.6	0.0	4.8	8.6
Max	25.5	11.5	8.4	26.9	35.5
Standard Error	0.41	0.22	0.17	0.43	0.47

^aTotal live cover is the combination of live sagebrush cover and live other shrub cover.

^bAll shrub cover is the combination of live and dead sagebrush cover and all other shrub cover.

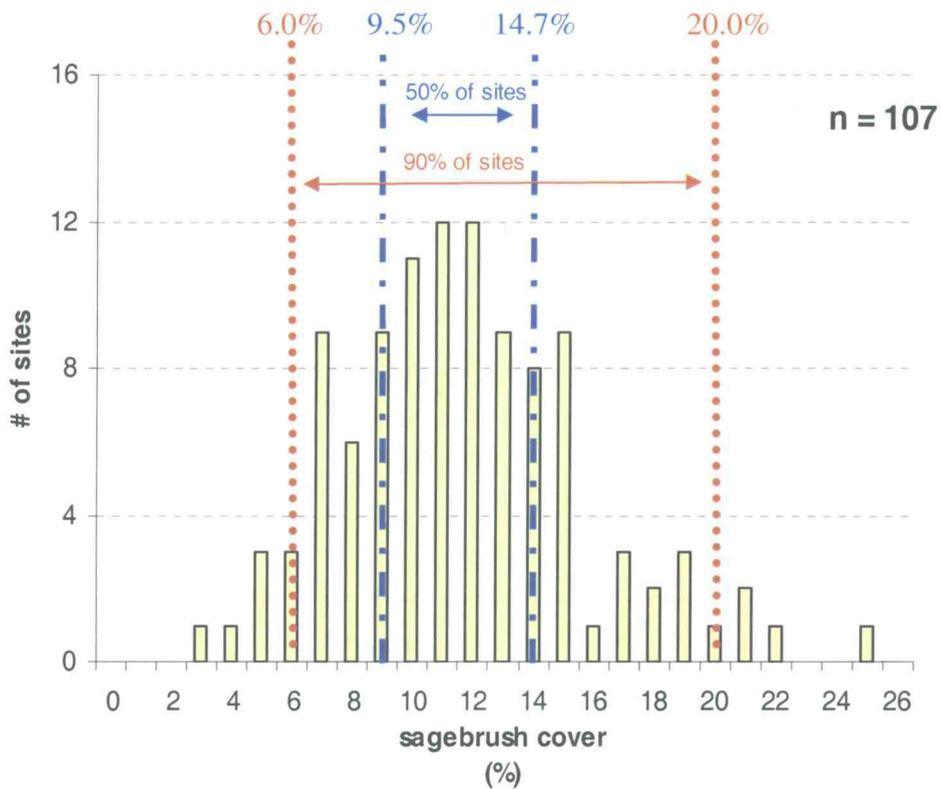


Figure 3.3. The number of sites that produced certain quantities of sagebrush cover. The x-axis labels are percentage categories.

Table 3.3. Wyoming big sagebrush association stand cover values previously reported.

ASSOCIATION	SAGEBRUSH COVER	LOCATION	REFERENCE
ARTRW8/FEID	7-25%	Eastern Oregon	Doescher et al. 1986
ARTRW8/STCO2	0.3-22%	Utah	Goodrich et al. 1999
ARTRW8/AGSP	5.2-7%	Jordan Crater Kipukas	Kindschy 1992
ARTRW8/STTH	4-13%	EOARC Burns, OR	File Data
ARTRW8/FEID	5-22%	EOARC Burns	File Data
ARTRW8/AGSP	6.5% average	Mill, Utah	West and Hassan 1985

ARTRW8 = Wyoming big sagebrush, STCO2 = needle-and-thread grass, AGSP = bluebunch wheatgrass, STTH = Thurber's needlegrass, and FEID = Idaho fescue. EOARC = Eastern Oregon Agricultural Research Center

Wyoming big sagebrush association classification

Species composition was represented by 238 plant species including 17 shrub species, 2 tree species, 19 perennial grass species, 5 annual grass species, 127 perennial forb species, and 68 annual forb species (Appendix 3). Initially, cluster analysis by species composition was used to group similar plant communities into associations. The National Vegetation Classification Standard (The Nature Conservancy 1994) defines an association as a physiognomically uniform group of

vegetation stands that share one or more diagnostic (dominant, differential, indicator, or character) overstory and understory species. Though different associations were formed, none could easily be recognized in the field. No indicator species were consistently present or exclusive for any of the associations. However some clustering of sites did result from the occurrence of dominant perennial bunchgrasses. For a vegetation classification system to be useful, it must be uncomplicated and easily implemented in the field. Building from some of the patterns we observed in the cluster analysis and our desire for simplicity, we formed five associations based on dominant late seral perennial bunchgrass species. Passey et al. (1982) reported similar difficulties with classifying vegetation groups with cluster analysis, which resulted in them using their field experience to designate associations.

The Wyoming big sagebrush alliance (ARTRW8) plant associations we classified were: ARTRW8/AGSP (*Agropyron spicatum* (Pursh) Schibn. & Smith, bluebunch wheatgrass), ARTRW8/STTH (*Stipa thurberiana* Piper, Thurber's needlegrass), ARTRW8/FEID (*Festuca idahoensis* Elmer, Idaho fescue), ARTRW8/STCO2 (*Stipa comata* Trin. & Rupr., needle-and-thread), and ARTRW8/AGSP-STTH (a co-dominance of bluebunch wheatgrass and Thurber's needlegrass). Our classification was similar to previous systems. Hironaka et al. (1983) habitat type descriptions for southern Idaho included ARTRW8/AGSP and ARTRW8/STTH. Dissimilar to our classification, they found ARTRW8/POSA (Sandberg bluegrass) and ARTRW8/SIHY (*Sitanion hystrix* (Nutt.) J.G. Sm.) habitat types and considered mixtures of Thurber's

needlegrass with bluebunch wheatgrass to be members of the ARTRW8/AGSP habitat type. They also did not identify ARTRW8/FEID or ARTRW8/STCO2 habitat types. Our sampling was limited to relatively undisturbed, late seral Wyoming big sagebrush communities; thus, we didn't report any ARTRW8/SIHY or ARTRW8/POSA associations, because we did not sample communities dominated by lower seral perennial bunchgrasses. Doescher et al. (1986) identified and described an ARTRW8/FEID habitat type in eastern Oregon, and Passey et al. (1982) reported an ARTRW8/FEID community in their survey. Passey et al. (1982) also identified ARTRW8/AGSP and ARTRW8/STTH communities. The slight discrepancies between our classification and others should be expected due to differences among the regions where they were developed. Hironaka et al. (1983) and Passey et al. (1982) did not extend into eastern Oregon, and Doescher et al. (1986) only described one habitat type.

When referring to the association, only the dominant perennial grass code will be used in the remainder of this section. The AGSP association appeared to be the most abundant relatively intact, late seral association in the region, and was represented with 63 sites sampled. Other associations sampled included 16 STTH, 14 FEID, 7 STCO2, and 7 AGSP-STTH sites.

MRPP analysis indicated that forming associations by dominant perennial bunchgrass species successfully grouped similar sites together. Species composition within associations, after excluding dominant perennial bunchgrass species used for

grouping, was more homogenous than expected by chance ($p < 0.0001$, $A = 0.0325$). Sites within an association had similar species composition, while species composition varied among the 5 associations. Inclusion of the dominant perennial bunchgrass species in the analysis increased homogeneity within associations and increased heterogeneity between associations ($p < 0.0001$, $A = 0.1968$). Thus, the classification of the Wyoming big sagebrush alliance by dominant perennial grass was appropriate, simple, and useful. The historic classification of rangelands (Habitat Types, Cover Types, Range Sites, etc.) by dominant shrub and dominant perennial grass species remains a valid means of delineating associations in the Wyoming big sagebrush alliance.

Association vegetation characteristics

Functional group cover values were significantly different among associations (Table 3.4). Tall tussock perennial grass cover of the FEID association was almost twice that of any of the other associations. Sandberg bluegrass cover was less in the STCO2 association than the other associations. The STCO2 association also had the lowest perennial forb cover, ranging from eight to sixteen times less than the other associations. Annual grass cover was different between a few of the associations, but was generally very low. Annual grass cover was mainly composed of cheatgrass (*Bromus tectorum* L.), though native annual grasses (*Vulpia* sp.) were also present on

several sites. Cheatgrass presence on these relatively undisturbed areas may be a threat if fire disturbance occurs, especially in the STTH association (Bates et al. 2004).

High degrees of variability in functional group and total herbaceous cover values existed within and among plant associations (Fig. 3.4-3.8). Total herbaceous cover was significantly different among many of the associations (Table 3.4). The FEID association had the greatest total herbaceous cover, followed in order by the AGSP association, the AGSP-STTH association, the STTH association, and the STCO2 association. The STCO2 association produced less than half of herbaceous cover of the FEID association (Table 3.4). Grouping the Wyoming big sagebrush alliance into associations for management purposes is supported by the differences in the associations' ability to produce herbaceous cover. The differences in vegetation characteristics between associations indicate that management needs to be tailored to individual associations or be constrained by the least resilient association within a management unit. For example, Bates et al. (2004) reported that wildfire had a more negative, longer-lasting impact on herbaceous vegetation in the STTH than the AGSP association, but suggested efforts should be made to limit wildfires across the Wyoming big sagebrush alliance because STTH and AGSP associations are found in a mosaic across the landscape.

Unlike the herbaceous functional groups, Wyoming big sagebrush cover was not significantly different among most of the associations ($p > 0.05$) (Table 3.4).

Wyoming big sagebrush cover was greater in the AGSP-STTH than the STCO2 association ($p < 0.05$).

Table 3.4. Mean percent cover of functional groups by association with standard error.

Functional Groups	<u>Association</u>				
	<i>AGSP</i> n = 63 (%)	<i>STTH</i> n = 16 (%)	<i>STCO2</i> n = 7 (%)	<i>FEID</i> n = 14 (%)	<i>AGSP-STTH</i> n = 7 (%)
Sandberg bluegrass	6.0±0.27 c	4.8±0.37 bc	1.6±0.78 a	4.5±0.39 b	6.7±1.23 c
Tall Tussock Perennial Grass	11.9±0.46 b	8.8±0.36 a	11.0±1.97 ab	19.4±1.20 c	9.4±0.88 a
Annual Grass	0.8±0.22 b	0.4±0.24 ab	0.8±0.22 b	0.02±0.01 a	0.7±0.27 b
Perennial Forb	4.8±0.36 c	2.5±0.42 b	0.3±0.09 a	4.4±0.44 c	5.0±1.20 c
Annual Forb	0.6±0.11 ab	0.8±0.18 ab	0.2±0.06 a	0.4±0.10 ab	0.4±0.04 b
Total Herbaceous	24.1±0.77 b	17.1±0.86 a	13.9±2.44 a	28.7±1.26 c	22.1±2.12 abc
Wyoming big sagebrush	12.0±0.48 ab	13.5±0.91 ab	9.9±2.28 a	11.1±0.90 ab	16.8±2.44 b

Different lower case letters indicate significant ($p < 0.05$) differences among associations by functional group.

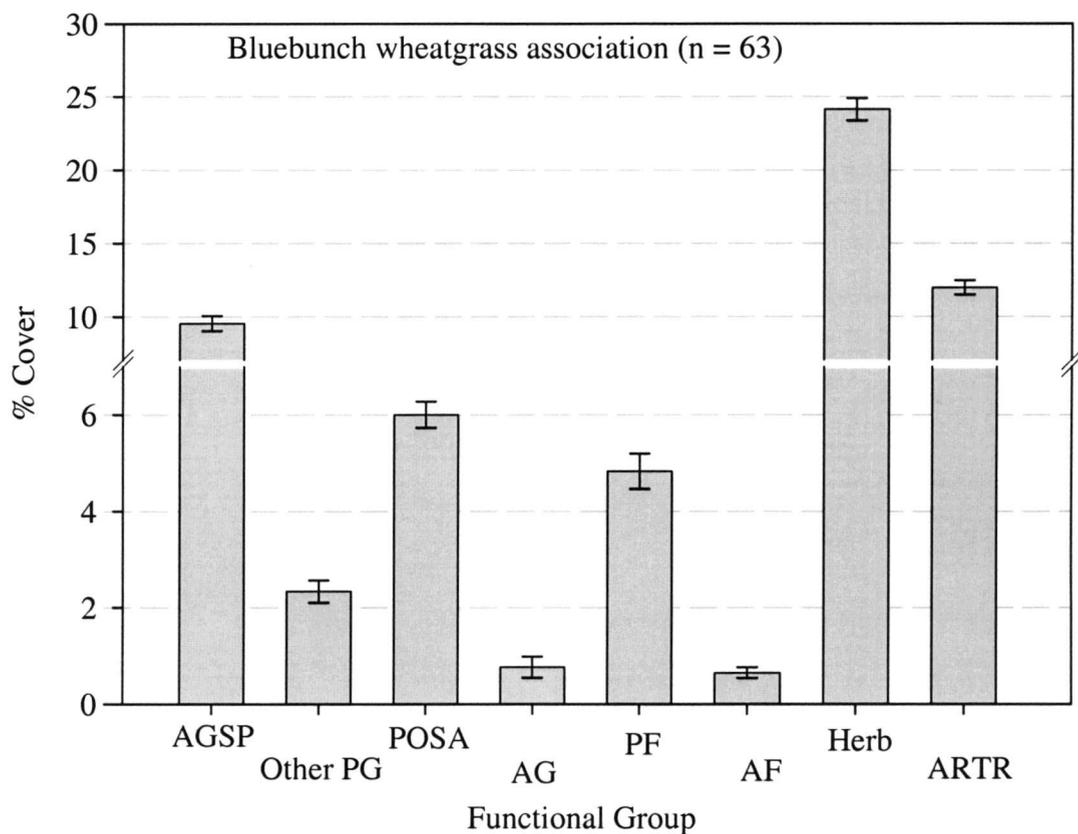


Figure 3.4. AGSP association's mean functional group cover values with standard error bars. AGSP = bluebunch wheatgrass, Other PG = Other Tall Tussock Perennial Grass, POSA = Sandberg bluegrass, AG = Annual Grass, PF = Perennial Forb, AF = Annual Forb, Herb = Total herbaceous, and ARTR = Wyoming Big Sagebrush.

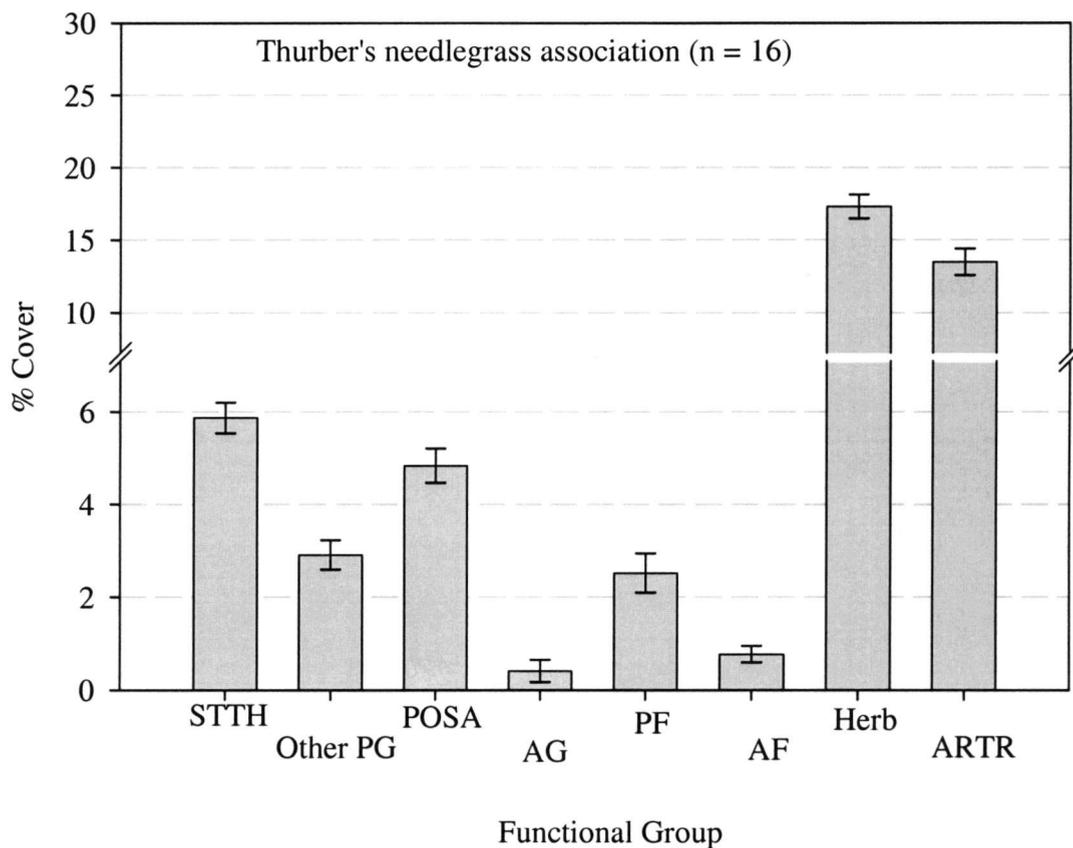


Figure 3.5. STTH association's mean functional group cover values with standard error bars. STTH = Thurber's needlegrass, Other PG = Other Tall Tussock Perennial Grass, POSA = Sandberg bluegrass, AG = Annual Grass, PF = Perennial Forb, AF = Annual Forb, Herb = Total herbaceous, and ARTR = Wyoming Big Sagebrush.

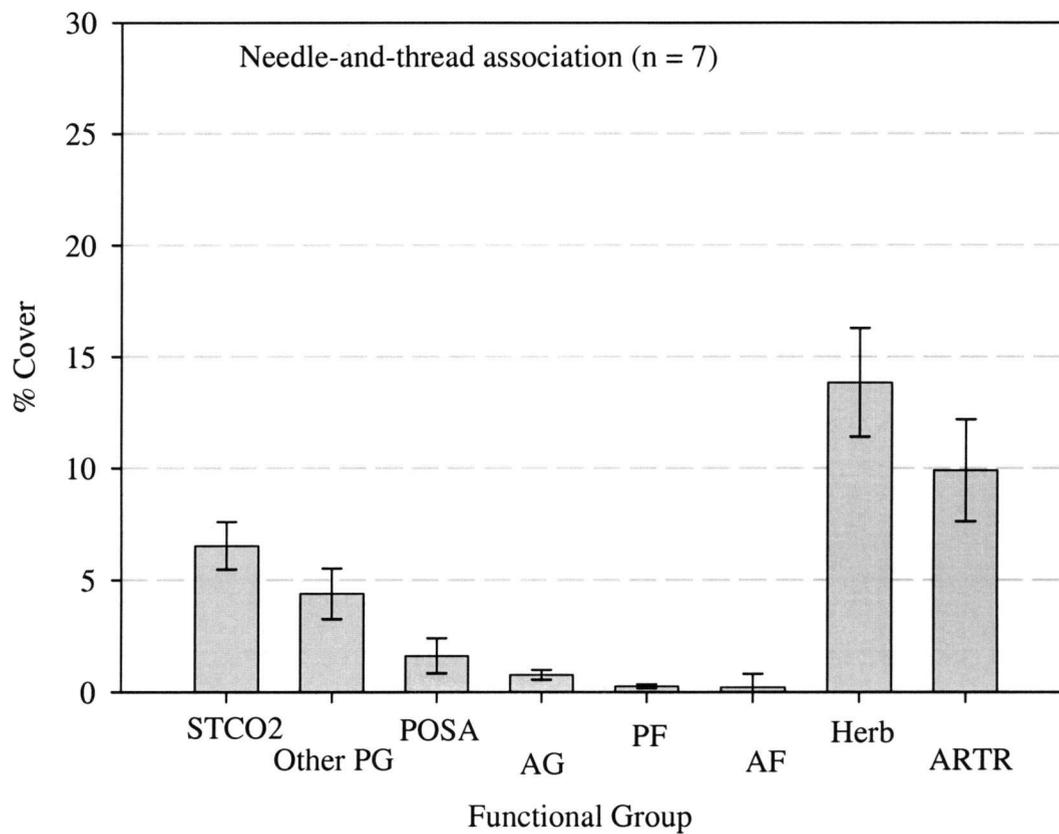


Figure 3.6. STCO2 association's mean functional group cover values with standard error bars. STCO2 = needle-and-thread, Other PG = Other Tall Tussock Perennial Grass, POSA = Sandberg bluegrass, AG = Annual Grass, PF = Perennial Forb, AF = Annual Forb, Herb = Total herbaceous, and ARTR = Wyoming Big Sagebrush.

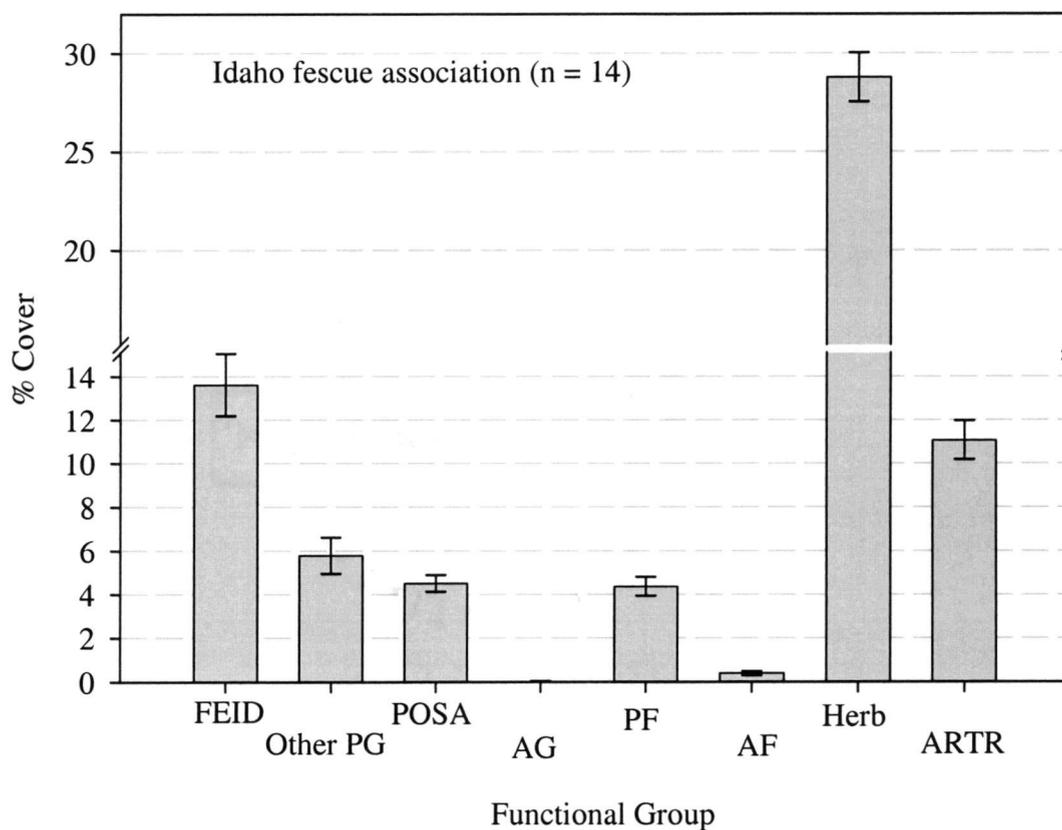


Figure 3.7. FEID association's mean functional group cover values with standard error bars. FEID = Idaho fescue, Other PG = Other Tall Tussock Perennial Grass, POSA = Sandberg bluegrass, AG = Annual Grass, PF = Perennial Forb, AF = Annual Forb, Herb = Total herbaceous, and ARTR = Wyoming Big Sagebrush.

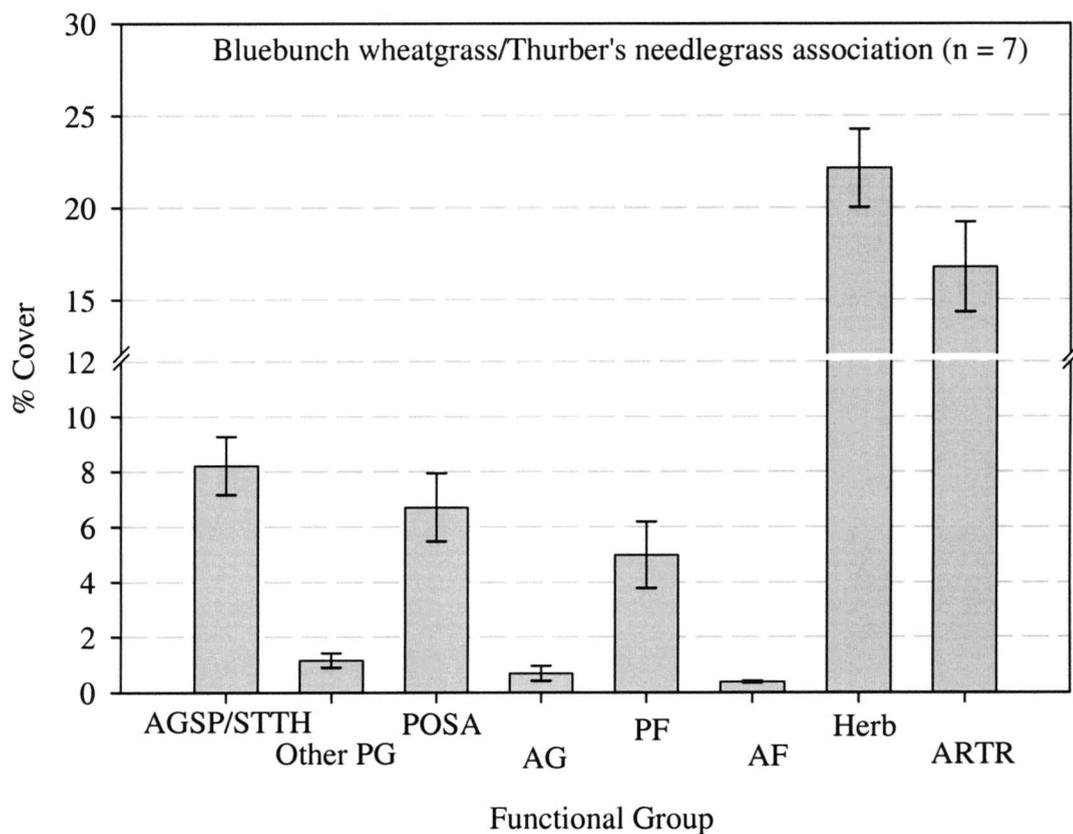


Figure 3.8. AGSP-STTH association's mean functional group cover values with standard error bars. AGSP-STTH = bluebunch wheatgrass-Thurber's needlegrass, Other PG = Other Tall Tussock Perennial Grass, POSA = Sandberg bluegrass, AG = Annual Grass, PF = Perennial Forb, AF = Annual Forb, Herb = Total herbaceous, and ARTR = Wyoming Big Sagebrush.

Management Implications and Conclusions

Differences in Wyoming big sagebrush associations' composition, functional group cover, and other vegetation characteristics (excluding perennial bunchgrasses used for grouping) indicate that biological potential varies by association.

Management and guidelines must recognize that potential vegetation characteristics vary across associations and within individual associations. Forming associations by dominant tall tussock perennial bunchgrass species is a convenient, practical, and informative classification of the Wyoming big sagebrush alliance that improves management by grouping sites with similar vegetation characteristics and potentials.

The vegetation requirements from the sage-grouse guidelines should not be used to manage the Wyoming big sagebrush alliance. The BLM et al. (2000) vegetation requirements were generally beyond the biological potential of the Wyoming big sagebrush alliance in eastern Oregon (Table 3.5). Connelly et al. (2000) vegetation requirements exceeded the potential of many of the sites sampled. Although sites may be capable of producing high vegetation cover values in one functional group, it is highly unlikely that they would produce high cover across several functional groups (Appendix 4). If the vegetation requirements from the guidelines are going to be applied at or above the stand level to manage the Wyoming big sagebrush alliance, then they need to be adjusted to better match the biological potentials of this alliance.

Table 3.5. Number and percent of high condition Wyoming big sagebrush sites by associations that met the guidelines habitat requirements.

Assoc.	# of Sites	<u>BLM et al. (2000)</u> <u>Guidelines</u>				<u>Connelly et al. (2000)</u> <u>Guidelines</u>			
		Nest	Opt. rear	Subopt rearing	Winter	Mesic Breed	Arid Breed	Brood-rearing	Winter
AGSP	63	0 (0%)	0 (0%)	21 (33%)	43 (68%)	0 (0%)	12 (19%)	43 (68%)	43 (68%)
STTH	16	0 (0%)	0 (0%)	3 (19%)	15 (93%)	0 (0%)	2 (13%)	9 (56%)	15 (93%)
STCO2	7	0 (0%)	0 (0%)	0 (0%)	3 (43%)	0 (0%)	0 (0%)	1 (14%)	3 (43%)
FEID	14	0 (0%)	0 (0%)	3 (21%)	9 (64%)	0 (0%)	1 (7%)	9 (64%)	9 (64%)
AGSP/ STTH	7	0 (0%)	0 (0%)	5 (71%)	5 (71%)	0 (0%)	4 (57%)	5 (71%)	5 (71%)
TOTAL	107	0 (0%)	0 (0%)	32 (30%)	75 (70%)	0 (0%)	19 (18%)	68 (64%)	75 (70%)

Surveys of other sagebrush species and subspecies need to occur to prevent disagreement and conflict over their potentials. Critical to our region would be surveys of the mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle), basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*), and low sagebrush (*Artemisia arbuscula* Nutt.) alliances.

Any attempt to develop vegetation requirements for the sagebrush biome should include the potential range of vegetation characteristics across the Wyoming big sagebrush alliance. Our survey of the vegetation characteristics of the Wyoming big sagebrush alliance in the High Desert, western Snake River, and Humboldt ecological provinces provides information that can be used for this purpose.

Guidelines, in general, could be improved by acknowledging that range and forest lands need to be managed for multiple species. More comprehensive guidelines need to be developed for the sagebrush alliances that direct management for multiple sagebrush obligate and facultative wildlife species. Otherwise, we may manage sagebrush communities for one wildlife species at the expense of others.

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CHAPTER 4

**RELATIONSHIPS AMONG ENVIRONMENTAL AND VEGETATION
CHARACTERISTICS: WYOMING BIG SAGEBRUSH ALLIANCE**

Kirk W. Davies, Jonathan D. Bates, and Richard F. Miller

RELATIONSHIPS AMONG ENVIRONMENTAL AND VEGETATION CHARACTERISTICS: WYOMING BIG SAGEBRUSH ALLIANCE

Abstract

The Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance is the most extensive of the big sagebrush complex in the Intermountain West and is characterized by a wide range of environments and vegetation heterogeneity. However, the influence of environmental factors to vegetation heterogeneity has received limited attention. Describing relationships among environmental and vegetation characteristics may prove useful for restoration and management efforts. Environmental and vegetation characteristics were measured on 107 relatively undisturbed, late seral Wyoming big sagebrush sites across the northwestern portion of the sagebrush biome. Variation in perennial grass, perennial forb, and total herbaceous cover was correlated with incidental radiation and soil characteristics, particularly soil texture in the upper 15 cm of the profile. Total herbaceous cover variation was better explained by environmental factors ($p < 0.0001$, $r^2 = 0.52$) than any other vegetation characteristic. Vegetation structural characteristics (sagebrush height, sagebrush volume, sagebrush density, and visual obstruction) exhibited weak or no relationships with measured environmental variables. The relationships among environmental factors and vegetation

characteristics across the Wyoming big sagebrush alliance were found to have limited use for management because they did little to explain vegetation heterogeneity. The limited correlation among environmental factors and vegetation heterogeneity is due to the large ecological amplitude and ecotypic variation of many of the plant species found throughout this region.

Introduction

Environmental factors (soil, elevation, precipitation, etc.) have been used successfully to distinguish between sagebrush (*Artemisia*)¹ alliances (Winward 1980, Hironaka et al. 1983, Swanson et al. 1986, Tisdale 1994). They have not been used to explain or predict vegetation heterogeneity within a specific big sagebrush alliance. Insight into relationships between environmental factors and vegetation composition, cover, and structure in alliances would assist land managers in developing guidelines, creating management objectives and goals, and integrate habitat requirements for sagebrush obligates with the biological potentials of individual stands. Understanding interactions among environmental characteristics and vegetation could improve management's ability to prioritize habitat restoration. For example, when restoring vegetation communities to meet habitat requirements of a specific wildlife species,

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. *Flora of the Pacific Northwest*. University of Washington Press. Seattle, WA. 730 p.

managers could exclude sites, based on environmental factors, which do not have the potential to meet habitat requirements.

In the sagebrush biome, aside from Passey et al. (1982) and Jensen (1990), few studies have investigated the relationship among environmental factors and vegetation characteristics. However, these studies were limited by: 1) a lack of replication to address the variability of vegetation and environmental characteristics within an alliance, as in the case of both Passey et al. (1982) and Jensen et al. (1990); and 2) vegetation measurements were only weight estimates, as in the case of Jensen et al. (1990).

Classification systems (i.e. Habitat Types, Cover Types, plant associations, and Ecological Sites) recognize differences in plant communities, but generally lack correlation with environmental factors. Because of their broad descriptive nature, Habitat Types and Cover Types offer little detailed information on relationships among vegetation and environmental characteristics. These classifications are based on potential natural vegetation. Jensen et al. (1990) advised caution when using Cover Types to infer a site's underlying soil properties, because basing Cover Types on site and soil characteristics was proven to be highly inconsistent. This is because many diagnostic species used in the classification process possess wide ecological amplitudes and ecotypic variation (Passey et al., 1982, Doescher et al., 1985, West, 1988). Plant associations are based on the dominant overstory species and one or two dominant understory diagnostic species. Although useful, these delineations can occur

across a wide array of soils and other environmental characteristics. Because plant associations are based on species present, individual sites can support more than one plant association. Ecological Sites (Natural Resource Conservation Service (NRCS) 1997) can be incorporated under Habitat Types as more discrete units detailing soil type, productive potential, major uses, and expected associated natural plant community for the site. A major limitation of the Ecological Site classification, as inferred from research results (Jensen et al. 1990, Passey et al. 1982), is that potential natural communities can be found on a wide range of soil types and are production-oriented. The lack of adequate descriptions of vegetation composition, cover, and structure, which are important to wildlife, limits Ecological Site classification value for evaluating or describing wildlife habitat.

The purpose of this study was to determine if environmental variables could be used to further refine predictions of vegetation characteristics within alliances. The Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) alliance was selected because 1) it is the most extensive of the big sagebrush (*A. tridentata* Nutt.) complex in the Intermountain West (Tisdale 1994, Miller and Eddleman 2000), and 2) there is a lack of information describing heterogeneity of vegetation composition, cover, and structure relationships to environmental characteristics across this alliance.

The objectives of this study were to: 1) identify key environmental attributes correlated with plant species composition; 2) evaluate correlations between

environmental factors and vegetation cover; and 3) determine relationships between environmental variables and vegetation structure across the Wyoming big sagebrush alliance in part of the northwest portion of the sagebrush biome.

Method and Statistics

Site Selection

During February, March, and April of 2001 and 2002, Bureau of Land Management (BLM) offices in Lakeview, Vale, and Burns, OR and Winnemucca, NV were contacted to obtain locations of Wyoming big sagebrush communities considered to be in high ecological condition in the High Desert, Humboldt, and western Snake River ecological provinces. We sampled 107 sites across this area (Fig. 4.1). Sites were sampled from late May to the first part of July. Sites were selected in late seral condition and according to the following criteria; 1) the understory was dominated by native, tall tussock perennial bunchgrasses and forbs, 2) exotic/introduced species were a minor to nonexistent component, 3) there was minimal to no visual impacts from livestock use with evidence of restricted livestock accessibility (Passey et al. 1982), and 4) stands were dominated by mature sagebrush with limited recruitment of new shrubs. Soil descriptions were used to determine Ecological Sites to further ensure sites were in late seral condition. Our site selection criteria were stricter than those used for rangeland health reference sites (Pellant et al. 2005). We sampled in

areas with an array of different site characteristics (e.g. slope, elevation, aspect, soil, and dominant grass species) to capture vegetation and environmental variation across the Wyoming big sagebrush alliance.

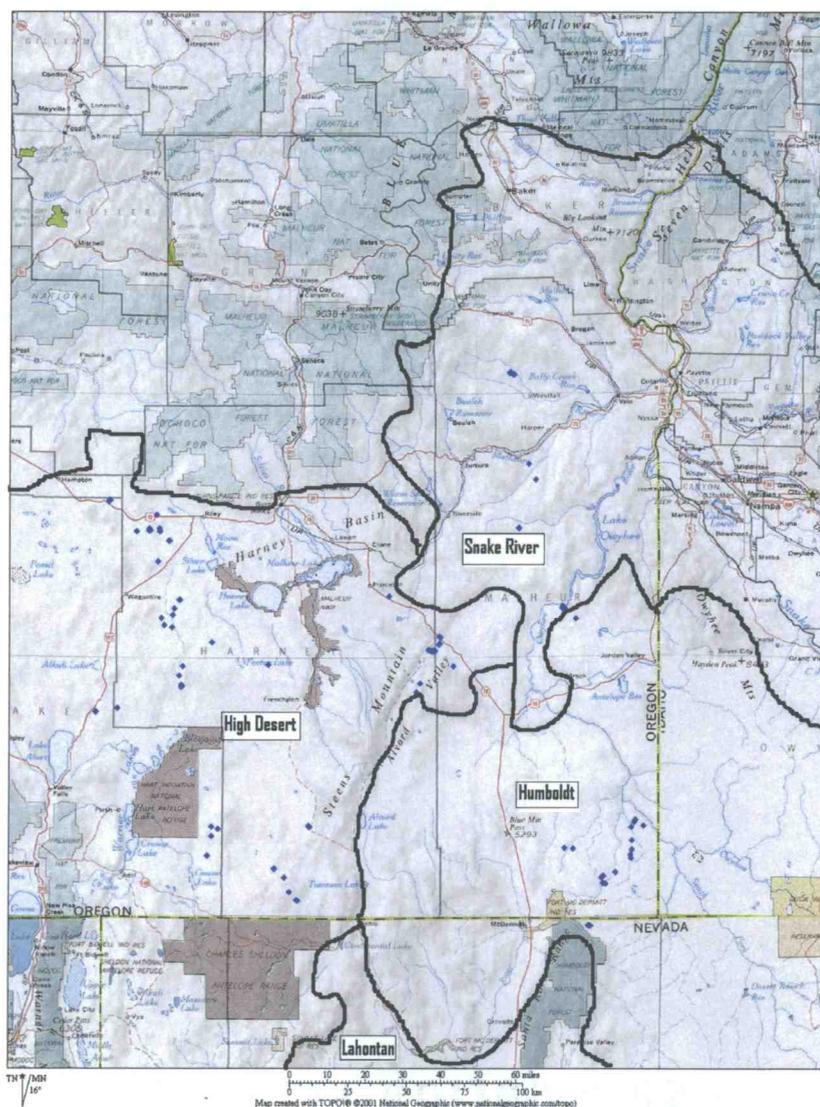


Figure 4.1. Study site locations. Blue diamonds represent areas where Wyoming big sagebrush sites were sampled. Ecological province boundaries (bold black lines) were derived from Anderson et al. (1998) and Bailey (1994).

Sampling

To investigate relationships between environmental factors and vegetation, many environmental and vegetation characteristics were measured (Table 4.1).

Table 4.1. Environmental factors and vegetation characteristics measured at each site.

Vegetation Characteristics	Environmental Factors
Shrub Cover	Precipitation
Shrub Density	Elevation
Sagebrush Canopy Volume	Soil Water Holding Capacity
Sagebrush Height	Soil Texture
Herbaceous Cover	Effective Rooting Depth
Herbaceous Composition	Depth to Bt horizon
Horizontal Visual Obstruction	Soil Total Carbon and Nitrogen
	Soil pH
	Soil Depth
	Slope
	Aspect
	Landform
	Incidental Radiation
	Universal Transverse Mercator

Vegetation Characteristics

At each site, five 50 m transects were laid out at 20 m intervals. Shrub canopy cover was measured using the line intercept method (Canfield 1941). Canopy gaps up to 15 cm were included in canopy cover estimates. Sagebrush density was measured using five 2 X 50 m belt transects. Average sagebrush canopy volumes were calculated by randomly measuring the height and two intersecting diameters of 50 sagebrush plants at each site (Rittenhouse and Sneva 1977).

Herbaceous canopy cover was visually estimated by species using 0.2 m² (40 X 50 cm) frames located at 3 m intervals along the transect lines (starting at 3 m and ending at 45 m) resulting in 15 frames per transect and 75 frames per site. Herbaceous composition was determined using species canopy cover.

Horizontal visual obstruction, an estimate of horizontal concealment habitat for wildlife, was estimated using a 1 m² board (Bunnel 2000). The board was stratified into thirds (lower = 0 - 33.3 cm, middle = 33.3 - 66.6 cm, and upper = 66.6 - 100 cm) along the vertical axis, with each stratum divided into 12 equal size squares (16.7 cm x 16.7 cm). Squares were alternately colored white and black. Visual obscurity was measured at 30 cm height by eye 5 m from the 1 m² board. Measurements were taken every 10 m on both sides of established transect lines, starting at the 5 m point. This resulted in 10 measurement locations (5 per side) per transect, yielding a total of 50 per plot.

Environmental Factors

Precipitation (long-term estimated average) and elevation for each plot were determined from climate (NRCS 1998) and topographic (Geological Survey 1967) maps of the area. Precipitation data was at a coarse scale (5 cm precision) within a relatively narrow band of precipitation (majority of sites received between 20 and 30 cm). A soil pit was dug to a restrictive layer at each site. Soil depth to bedrock, hard pan, or other restrictive layer was measured. Color, texture, thickness, structure, carbonates, and rock fragment percentage of horizons above the restrictive layer were described in the field. Water holding capacity was estimated using the texture and thickness of each horizon minus the rock fragment (Brady and Weil 2002). Effective rooting depth was measured in each soil pit. Depth to Bt horizon was measured on all sites where present. When a Bt horizon was not present, depth of the soil was used in the analysis, because that would be where soil moisture and roots downward movement would be restricted. The surface was inspected for a crust and vesicular pores. Three soil sub-samples from the surface to a depth of 15 cm were randomly taken between shrubs. Sub-samples were compiled, thoroughly mixed, and then tested for total carbon, total nitrogen content, and pH.

Slope and aspect were determined in the field using a clinometer and compass. Each site's Universal Transverse Mercator (UTM) coordinates and landform were

recorded. Incident radiation was estimated from an equation developed by McCune and Keon (2002)¹.

Statistical Analysis

Nonmetric Multidimensional Scaling (NMS) using PC-ORD ver. 4 (1999) was used to identify environmental variables correlated to plant species composition. Prior to employing NMS, rare species (species occurring in less than 3 sites) were removed from the analysis. Deleting rare species reduces noise in large data sets and often enhances detection of relationships between environmental factors and community composition (McCune and Grace 2002). Species cover values were log transformed to improve the amount of variation explained by the NMS ordination. To log transform zeros, a small number was added to all data points and then its log was subtracted from all data points after transformation (McCune and Grace 2002). Random starting location and Sorensen's distance measurement were used with the NMS autopilot slow and thorough method.

Multiple linear regression using S-Plus (2000) was used to determine correlations among environmental factors and vegetation cover and structure. Environmental factors (explanatory variables) that were not influential were not included in the final model explaining the variation in the vegetation characteristic (response variable) of interest. This model selection was performed with a stepwise regression procedure.

¹ Incident radiation ($\text{MJ cm}^{-2} \text{ yr}^{-1}$) = $0.339 + 0.808(\cos(L) \times \cos(S)) - 0.196(\sin(L) \times \sin(S)) - 0.482(\cos(A) \times \sin(S))$, where A = folded slope in radians east of north, S = Slope in radians, L = Latitude radians north.

For multiple linear regression, herbaceous cover was grouped into five functional groups: Sandberg bluegrass (*Poa sandbergii* Vasey), tall perennial grass, annual grass, perennial forbs, and annual forbs. The purpose of using functional groups is to combine species that respond similarly to environmental perturbation and to reduce data to a simpler form for analysis and presentation (Boyd and Bidwell 2002). Functional groups simplify analysis and permit comparisons among sites with different species composition. Total herbaceous cover was the sum of all herbaceous species.

Results

Environmental Factors Correlation to Plant Species Composition

The NMS final solution was 3-dimensional and explained 81% (cumulative $r^2 = 0.814$, Axis 1 $r^2 = 0.218$, Axis 2 $r^2 = 0.289$, and Axis 3 $r^2 = 0.308$) of the variation in species composition. The NMS final solution explained more variation than expected by chance (Monte Carlo test, $p < 0.0001$). Final stress for the 3-dimensional solution was 16.978 and final instability was 0.00001 with 151 iterations. Variation in plant species composition was related mainly to soil characteristics as shown by the axes' correlations with soil texture, soil nutrients, and depth to a Bt horizon. Percent clay in the upper 15 cm of soil was positively correlated, while sand was negatively correlated

with Axis 1 ($r^2 = 0.340$ and 0.333 , respectively) (Fig. 4.2). Slope was positively correlated with Axis 2 ($r^2 = 0.281$) (Fig. 4.3). Depth to a Bt horizon and percent sand in the upper 15 cm of soil were positively correlated ($r^2 = 0.188$ and 0.154 , respectively), while percent nitrogen, carbon, and silt in the upper 15 cm of soil were negatively correlated with Axis 3 ($r^2 = 0.245$, 0.217 , and 0.153 respectively). Aspect, precipitation, landscape position, elevation, incidental radiation, soil pH in the upper 15 cm, effective rooting depth, and latitude had limited correlations with any axes ($r^2 < 0.141$).

Perennial bunchgrasses were strongly correlated ($r^2 \geq 0.125$) with one or more axis(es) (Table 4.2). Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) and needle-and-thread (*Stipa comata* Trin. & Rupr.) were strongly correlated with all three axes. Soil surface texture was one of the most important variables in determining perennial grass species composition on a site. As clay increased and sand decreased in the upper 15 cm along Axis 1, Sandberg bluegrass and bluebunch wheatgrass cover increased, while prairie junegrass (*Koeleria cristata* auct. p.p. non Pers) and needle-and-thread cover decreased. On sites with more sand and less silt or clay in upper horizons, needle-and-thread was more prevalent than bluebunch wheatgrass and Sandberg bluegrass. Idaho fescue also appears to decrease and Indian ricegrass (*Oryzopsis hymenoides* (Roemer & J.A. Schultes) Ricker ex Piper) increases as soil surface texture becomes sandier and less silty. Bluebunch wheatgrass and Idaho fescue (*Festuca idahoensis* Elmer) cover increased as degree of slope increased

along Axis 2, while squirreltail (*Sitanion hystrix* (Nutt.) J.G. Sm.), needle-and-thread, and Thurber's needlegrass (*Stipa thurberiana* Piper) cover decreased. As the percent of sand increased and nitrogen, silt, and carbon decreased in the upper 15 cm of the soil profile, and depth to the Bt horizon increased along Axis 3, Sandberg bluegrass, bluebunch wheatgrass, Idaho fescue cover decreased, while needle-and-thread, Indian ricegrass, and cheatgrass (*Bromus tectorum* L.) cover increased.

Perennial forb composition appears to be largely influenced by soil surface texture. More perennial forb species were strongly correlated with Axis 1 than both the other axes combined (Table 4.2). Percentages of sand and clay in the upper 15 cm of the soil profile appeared to be two of the important factors influencing perennial forb composition. No perennial forb species were strongly correlated with Axis 2. Velvet lupine (*Lupinus leucophyllus* Dougl. ex Lindl.), Hood's phlox (*Phlox hoodii* Richards) and long-leaf plox (*Phlox longifolia* Nutt.) were negatively correlated with Axis 3. Only four annual forbs species had strong correlations with any of the axes (Table 4.1). Three species were correlated with Axis 2 and one with Axis 1.

Environmental Factors and Vegetation Cover

Several environmental factors were correlated with vegetation cover characteristics ($p < 0.05$). However, no interactions among environmental variables were correlated with vegetation cover in any of the models tested ($p > 0.05$).

Sandberg bluegrass cover (POSA) was positively correlated with increasing percent silt (Si) in the upper 15 cm of the soil profile and negatively correlated with increasing incident radiation (IR) and depth (cm) to Bt horizon (Bt) ($p = 0.006, 0.002,$ and 0.020 , respectively). The regression model is as follows, with standard errors in parentheses below the corresponding coefficients:

$$\text{POSA} = 10.74 + 0.08(\text{Si}) - 8.89(\text{IR}) - 0.2(\text{Bt})$$

$$(3.01) \quad (0.03) \quad (2.73) \quad (0.02)$$

Residual standard error = 2.06, $p = 0.0000007$, $r^2 = 0.26$

Tall tussock perennial grass cover (PG) was positively correlated with soil water holding capacity (SWHC) and was negatively correlated with incident radiation, percent sand (S) in the upper 15 cm of the soil profile, and Wyoming big sagebrush cover (ARTRW8) ($p = 0.0005, 0.0017, 0.0084,$ and 0.0258 , respectively). The regression model was:

$$\text{PG} = 32.15 + 0.36(\text{SWHC}) - 17.19(\text{IR}) - 0.10(\text{S}) - 0.21(\text{ARTRW8})$$

$$(5.20) \quad (0.10) \quad (5.32) \quad (0.04) \quad (0.09)$$

Residual standard error = 3.97, $p = 0.0000002$, $r^2 = 0.30$

Perennial forb cover (PF) was negatively correlated with incident radiation and depth to Bt horizon ($p = 0.0001$ and < 0.0001 , respectively). The regression model was:

$$\text{PF} = 17.16 - 13.19(\text{IR}) - 0.04(\text{Bt})$$

$$(2.82) \quad (3.14) \quad (0.01)$$

Residual standard error = 2.45, $p = 0.0000002$, $r^2 = 0.25$

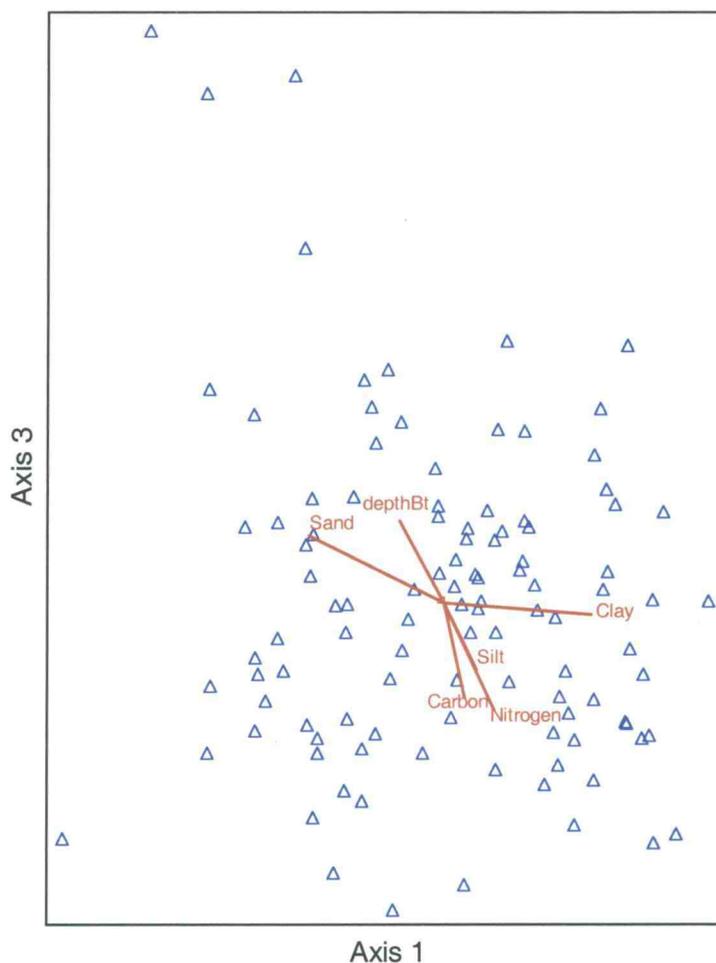


Figure 4.2. Nonmetric Multidimensional Scaling of sites (blue triangles) in species space along axis 1 and 3 with some of the correlated environmental factors. Direction of red lines indicates positive or negative correlation and length traversed along an individual axis depends on the strength of the correlation to that axis. Sand in the upper 15 cm of the soil profile was positively correlated with axis 3 and negatively correlated with axis 1. Clay in the upper 15 cm of the soil profile was positively correlated with axis 1 and had almost no correlation with axis 3. Nitrogen, carbon, and silt in the upper 15 cm of the soil profile were negatively correlated with axis 3 and had little correlation with axis 1. Depth to Bt horizon was positively correlated with axis 3 and had little correlation with axis 1.

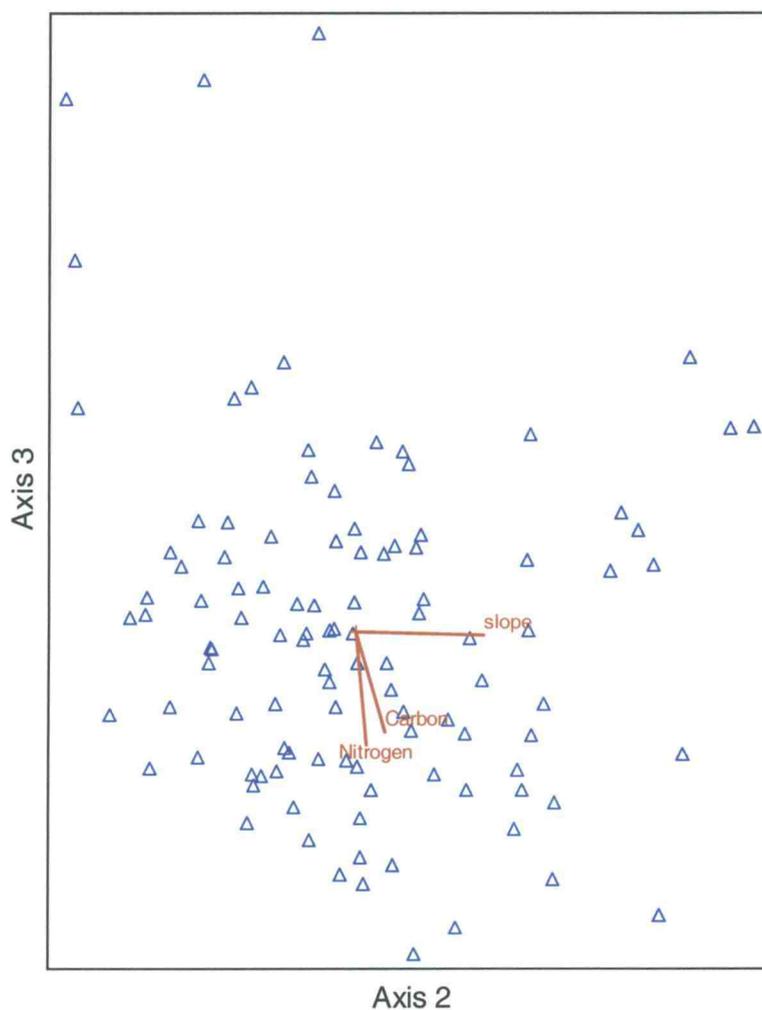


Figure 4.3. Nonmetric Multidimensional Scaling of sites (blue triangles) in species space along axis 2 and 3 with some of the correlated environmental factors. Direction of red lines indicates positive or negative correlation and length traversed along an individual axis depends on the strength of the correlation to that axis. Slope was positively correlated with axis 2 and had almost no correlation with axis 3. Nitrogen and carbon in the upper 15 cm of the soil profile were both negatively correlated with axis 3 and had little or no correlation with axis 2. Nitrogen was more negatively correlated with axis 3 than carbon.

Table 4.2. Plant species strongly correlated ($r^2 \geq 0.125$) with at least one of Nonmetric Multidimensional Scaling solution's axes.

Species	Axis 1 (r^2)	Axis 2 (r^2)	Axis 3 (r^2)
Perennial Grass			
<i>Poa sandbergii</i>	0.133	*	0.374 (-)
<i>Agropyron spicatum</i>	0.147	0.281	0.150 (-)
<i>Festuca idahoensis</i>	*	0.137	0.212 (-)
<i>Koeleria cristata</i>	0.186 (-)	*	*
<i>Oryzopsis hymenoides</i>	*	*	0.210
<i>Sitanion hystrix</i>	*	0.634 (-)	*
<i>Stipa comata</i>	0.125 (-)	0.126 (-)	0.365
<i>Stipa thurberiana</i>	*	0.343(-)	*
Annual Grass			
<i>Bromus tectorum</i>	*	0.155	0.440
Perennial Forb			
<i>Agoseris grandiflora</i>	0.226	*	*
<i>Astragalus obscurus</i>	0.205	*	*
<i>Crepis acuminata</i>	0.286 (-)	*	*
<i>Crepis occidentalis</i>	0.376	*	*
<i>Leptodactylon pungens</i>	0.165 (-)	*	*
<i>Lomatium macrocarpum</i>	0.144	*	*
<i>Lupinus leucophyllus</i>	*	*	0.165 (-)
<i>Phlox hoodii</i>	0.258 (-)	*	0.140 (-)
<i>Phlox longifolia</i>	0.425	*	0.158 (-)
Annual Forb			
<i>Blepharipappus scaber</i>	*	0.172	*
<i>Collomia linearis</i>	0.167	*	*
<i>Draba verna</i>	*	0.265	*
<i>Epilobium paniculatum</i>	*	0.153	*
Shrub			
<i>Chrysothamnus nauseosus</i>	*	0.202	*
<i>Chrysothamnus viscidiflorus</i>	0.155 (-)	*	*

Asterisk (*) indicates species weakly correlated with that axis ($r^2 < 0.125$).

Annual forb and annual grass cover were not associated with any measured environmental variables ($p > 0.05$).

Total herbaceous cover (THerb) was positively correlated with soil water holding capacity and negatively correlated with incidental radiation, depth to Bt horizon, and percent sand in the upper 15 cm of the soil profile ($p = 0.0001, < 0.0001, 0.0001, \text{ and } 0.0008$, respectively). More variation in total herbaceous cover was explained by environmental factors than any of the individual herbaceous functional group's cover.

The regression model was:

$$\text{THerb} = 63.34 + 0.49(\text{SWHC}) - 38.25(\text{IR}) - 0.08(\text{Bt}) - 0.17(\text{S})$$

$$(6.13) \quad (0.12) \quad (6.27) \quad (0.02) \quad (0.05)$$

Residual standard error = 4.73, $p < 0.0000001$, $r^2 = 0.52$

Wyoming big sagebrush cover (ARTRW8) was positively correlated with effective rooting depth (ERD) and negatively correlated with percent sand in the upper 15 cm of the soil profile ($p = 0.002$ and 0.004 , respectively). The regression model was:

$$\text{ARTRW8} = 15.50 + 0.04(\text{ERD}) - 0.12(\text{S})$$

$$(1.84) \quad (0.01) \quad (0.04)$$

Residual standard error = 7.54, $p = 0.0009$, $r^2 = 0.12$

Environmental Factors and Vegetation Structure

Correlations between measured environmental variables and vegetation structure were generally weak or not significant. Variation in Wyoming big sagebrush density (individuals/ha), sagebrush average volume (m^3), total visual obstruction (average of

the strata), and individual stratum of visual obstruction (# of squares blocked per transect side) explained by environmental variables did not exceed 10% ($r \leq 0.10$) (Table 4.3). Average mature sagebrush height (cm) was not correlated with any of the environmental factors measured ($p > 0.05$).

Table 4.3. Regression models for vegetation structure.

Regression Model w/ standard errors in parentheses below coefficients	Residual Standard Error	P- value	r^2
Sagebrush density = 3090.78 + 2.23(Elev) – 39.87(S) (1600) (0.96) (15.68)	1647	0.0038	0.10
Sagebrush volume = 1.27 – 0.12(pH) (0.29) (0.04)	0.13	0.0070	0.07
Total visual obstr. = 52.04 – 0.009(Elev) + 0.03(Depth) (5.65) (0.004) (0.02)	6.01	0.0070	0.10
Lower visual obstr. = 71.80 - 1.968(pH) (5.09) (0.75)	2.34	0.0101	0.06
Middle visual obstr. = 63.19 – 0.013(Elev) (7.30) (0.005)	8.26	0.0099	0.07
Upper visual obstr. = 44.32 – 2.36(ppt) + 0.05(Depth) (9.79) (0.93) (0.03)	9.35	0.0061	0.10

Obstr. = obstruction, Elev = Elevation in m, S = percent sand, Depth = soil depth in cm, and ppt = precipitation in cm.

Discussion

Direct relationships between environmental factors and vegetation characteristics were limited. Incidental radiation (a function of slope, aspect, and latitude) and soil characteristics were the only environmental variables to explain any of the variation in vegetation functional group cover values. Admittedly, the amount of cover variation explained for some of the functional groups were very limited, or in the case of the annual forbs and grasses, insignificant. Other broad studies in the sagebrush steppe (Jensen et al. 1990, Passey et al. 1982) also found limited direct relationships among environmental factors and vegetation variability.

Texture-related soil characteristics (percent sand and silt in the upper 15 cm, and soil water holding capacity) and depth to a Bt horizon were the most repeatedly correlated soil factors with vegetation cover values. Their influence is probably related to the amount and length of time soil water is available for plant use. Soil texture exerts a major influence over infiltration rates and soil water retention (Brady and Weil 2002). For example, as sand content increases, the soil's ability to hold water and retain nutrients in a plant available form decreases (Brady and Weil 2002). The negative correlation between perennial forb cover and depth to the Bt horizon was probably related to water availability. Many perennial forbs native to this region of the Wyoming big sagebrush alliance have relatively shallow roots when compared to the tall tussock perennial bunchgrasses (personal observation); thus, perennial forbs

more readily benefit from water held above the Bt horizon. When the Bt horizon is deeper in the soil profile (i.e. beneath the roots of shallow-rooted plants), shallow-rooted perennial forbs would be less able to capitalize on this soil water. Sandberg bluegrass, also shallow-rooted, cover decreases as depth to the Bt horizon increases. With decreasing depth to a Bt horizon Sandberg bluegrass cover increases. Sandberg bluegrass may have a competitive advantage over deeper rooted species when the Bt horizon results in shallow root penetration. Shallow-rooted species have a competitive advantage on shallower soils (Passey et al. 1982). Variations in weather may modify or mask some effects of specific soil characteristics on vegetation cover (Passey et al. 1982), but there are some apparent relationships between vegetation cover values and soil properties.

The negative correlation of incidental radiation to perennial functional groups and total herbaceous vegetation cover is related in part to the influence of radiation on temperature. Higher incidental radiation results in warmer temperatures (McCune and Keon 2002), which increases evapotranspiration and may inhibit photosynthesis. Increased evapotranspiration would dry soil faster, thus plants would experience moisture stress earlier in the growing season. Decreases in water available to plants have been shown to limit photosynthesis (Lawlor and Cornic 2002, Wingler et al. 1999). When temperatures increase above 30°C, photosynthesis in C₃ plants tends to be inhibited (Devlin and Witham 1983). When photosynthesis is limited or inhibited, plant production, i.e. cover, is reduced.

Vegetation cover is also influenced by variables other than environmental factors. Competition interactions among plants can mask interactions between those plants and environmental variables. For example, Miller et al. (2000) found mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) cover declined to 80% of its maximum potential when juniper canopies were 50% of maximum potential tree cover. The negative correlation we found between perennial grass cover and Wyoming big sagebrush cover is another example of plant interactions influencing vegetation cover composition. This negative correlation indicates that concurrently maximizing the cover of both sagebrush and perennial grass is not possible. Rittenhouse and Sneva (1976) found that a 1% increase in Wyoming big sagebrush cover resulted in a decrease in desert wheatgrass (*Agropyron desertorum* (Fisch. ex Link) J.A. Schultes) production of 36.9 to 61.2 kg/ha.

The lack of correlation between annual plants and measured environmental variables is likely due to the effects of interannual variation in precipitation. Bates et al. (1998) and Bates (2004) found annual forbs to be the most responsive functional group to different precipitation patterns. West and Yorks (2002) found annual grass cover fluctuated greatly with annual precipitation.

More variation in total herbaceous than individual herbaceous functional groups cover was explained by the environmental factors. This may be due to individual functional group cover responding more to species interactions and/or individual species correlations to select environmental factors than total herbaceous cover. These

confounding effects were removed by focusing on total herbaceous cover. For example, with competition an increase in one plant species cover can result in a decrease in the cover of a competing species. When these species are from different functional groups, interactions between the functional group and environmental variables are obscured by the species interaction, as seen in Miller et al. (2000). They saw an inverse relationship between juniper and herbaceous cover in juniper encroached mountain big sagebrush/Thurber needlegrass associations. Similarly, Wall et al. (2001) saw a decrease in aspen cover with increased juniper cover in aspen stands being encroached by juniper. Individual functional group cover would vary more at different levels of juniper encroachment than total vegetation cover. Thus, total herbaceous cover potentially fluctuates less with competition than individual functional groups. Individual species or functional groups cover could also be more influenced by individual or combinations of environmental factors at a select site than total herbaceous cover. Passey et al. (1982) reported that environmental conditions favorable to one species were frequently unfavorable to another. Among sites with similar total herbaceous cover, individual functional groups cover may vary widely due to individual responses to environmental factors or competition. Though the influence of year-to-year climatic variation on total herbaceous cover was not accounted for in this study, the relationships we found can explain 50% of the variation in total herbaceous cover across relatively intact, late seral Wyoming big

sagebrush communities in our region. These relationships may be improved with more detailed temperature and precipitation data.

Functional groups cover as well as Wyoming big sagebrush cover and structure were not well explained by environmental factors. The wide ecological amplitude of plant species in the Wyoming big sagebrush alliance probably minimizes the influences of individual environmental factors. Jensen et al. (1990) suggested that ecotypic and subspecific variation within a species could also account for the weak relationships between environmental characteristics and vegetation. For example, Wyoming big sagebrush cover (Bates et al. 1998) and growth development (Svejcar et al. 2003) did not differ with three different precipitation patterns (Winter, Spring, and Current). Wyoming big sagebrush utilizes more of the soil profile than herbaceous species, thus mediating effects of individual soil characteristics. Shown et al. (1972) found sagebrush utilizes more water in August and September than grass, which suggests that spatial and temporal variation of summer precipitation may confound some of the relationships among specific soil characteristics or precipitation amounts and sagebrush cover.

Management Implications and Conclusions

Environmental factors have proven useful for differentiating among sagebrush alliances, but within the Wyoming big sagebrush alliance they appear to be limited in

their ability to be used as predictors of vegetation composition and cover. Only two general relationships between environmental factors and vegetation within the alliance are useful to management. First, needle-and-thread can be expected to be the dominant perennial bunchgrass cover on sandy soils. Second, environments with favorable soil characteristics (loamy surface texture, greater soil water holding capacity, shallow depth to Bt horizon, etc.) and lower incidental radiation can be expected to produce more total herbaceous cover than environments with higher incidental radiation and less favorable soil characteristics. Thus, vegetation characteristics are influenced by numerous factors and are not limited to environmental variables. This restricts our ability to use environmental characteristics to predict vegetation composition and structure.

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CHAPTER 5

**WYOMING BIG SAGEBRUSH EFFECTS ON MICROSITE AND
VEGETATION HETEROGENEITY**

Kirk W. Davies, Jonathan D. Bates, and Richard F. Miller

WYOMING BIG SAGEBRUSH INFLUENCE ON MICROSITE AND VEGETATION HETEROGENEITY

Abstract

The distribution of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) within plant communities creates subcanopy and interspace zones which can influence microsite characteristics and spatial arrangement of vegetation. We investigated the effects of sagebrush on microsite (environmental and soil) characteristics and vegetation in subcanopy and interspace zones in Wyoming big sagebrush communities. Sites were located at the Northern Great Basin Experimental Range (NGBER) (56 km west of Burns, OR) and Baker Pass (80 km southeast of Burns, OR). At the NGBER, Wyoming big sagebrush created microsite and vegetation differences between subcanopy and interspace zones. Compared to the interspace, subcanopy zones were characterized by: 1) moderated soil temperatures, 2) higher levels of soil organic matter, nitrogen, carbon, and water, and 3) greater herbaceous biomass, cover, and density. Zonal vegetation differences measured at the NGBER were not found at Baker Pass. The results suggest that the influence of Wyoming big sagebrush on spatial heterogeneity of herbaceous vegetation is site dependent.

Introduction

The presence of big sagebrush (*Artemisia tridentata* Nutt.)¹ in plant communities has generated recent debate regarding its role as a competitor or facilitator with associated herbaceous and woody vegetation (Welch and Criddle 2003). The best evidence for sagebrush's role as a facilitator has been characterized with several tree species. The establishment and growth of singleleaf pinyon (*Pinus monophylla* Torr. & Frém) (Callaway et al. 1996, Chambers 2001), mountain mahogany (*Cercocarpus ledifolius* Nutt.) (Schultz et al. 1996), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Patten 1969), and western juniper (*Juniperus occidentalis* Hook.) (Miller and Rose 1995) were enhanced when situated underneath sagebrush canopies. Factors that may contribute to this facilitation are an increased availability of soil nutrients and water, and a moderated micro-environment. Soil nutrient concentrations and availability, particularly nitrogen (N) and phosphorus (P) (Charley and West 1975, Doescher et al. 1984, Burke et al. 1987), and soil water content (Wight et al. 1992, Chambers 2001) have been reported to be greater under than between sagebrush canopies. Moderated soil temperature regimes under sagebrush (Pierson and Wight 1991, Chambers 2001) likely contribute to increased seedling establishment.

However, evidence for competitive/facilitative interactions among sagebrush and herbaceous species is more limited and results often conflict. Sagebrush is highly

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press. Seattle, WA. 730 p.

competitive for P relative to associated bunchgrasses (Caldwell et al. 1985, 1987, 1991), but may increase the availability of water to plants growing in the subcanopy via hydraulic lift (Caldwell and Richards 1989). Herbage production tends to increase two to threefold following sagebrush removal (Blaisdell 1953, Harniss and Murray 1973, Hedrick et al. 1966, Sneva 1972) suggesting a strong competitive interaction between sagebrush and herbaceous vegetation. However, Blaisdell (1953) and Peek et al. (1979) also reported no significant changes in herbage production after burning sagebrush rangeland. Kranitz and Caldwell (1995) reported no reduction in perennial grass root development grown under mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) canopies compared to plants grown in the interspace. Establishment of herbaceous plants was enhanced under sagebrush canopies relative to interspaces in sagebrush communities in North Dakota (Hazlett and Hoffman 1975) and Nevada (Eckert et al. 1986). The confounding conclusions from these studies may be a product of differing sites, year effects, and species/subspecies of sagebrush evaluated.

This study did not directly measure competitive/facilitative interactions among sagebrush and associated herbaceous vegetation. The approach of the study was to 1) describe the influence of sagebrush on micro-environments and the spatial arrangement of soil resource characteristics, and 2) evaluate the influence of subcanopy and interspace zones on herbaceous composition and productivity. Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & A.

Young) S.L. Welsh) communities were chosen for evaluation, because this alliance is the largest and most arid of the big sagebrush complex in the western United States. With increasing site aridity the spatial organization of vegetation and resources tends to become more concentrated into discrete patches (Schlesinger et al. 1990). Thus, by using a Wyoming big sagebrush community we expected that measurable spatial differences would be discovered for zonal micro-environments and resource distribution that would assist in explaining subcanopy and interspace herbaceous vegetation characteristics. We hypothesized that: 1) sagebrush presence creates micro-environmental (temperatures, relative humidity, photosynthetic active radiation, soil water, and nutrients) differences between subcanopies and interspaces, and 2) sagebrush creates zonal differences in resource availability to herbaceous vegetation, which 3) influences zonal variation in herbaceous vegetation composition and production.

Methods

Study Sites

Northern Great Basin Experimental Range (NGBER)

The Northern Great Basin Experimental Range (NGBER) is located in southeastern Oregon about 56 km west of Burns, OR. The study site at the NGBER receives on average 300 mm of precipitation annually (EOARC data file). Elevation

is approximately 1,400 m above sea level, and topography is flat (slopes $< 2^\circ$). Soil surface texture is sandy loam to loamy sand. Incidental radiation averages $0.93 \text{ MJ cm}^{-2} \text{ yr}^{-1}$. Wyoming big sagebrush is the dominant shrub and Thurber's needlegrass (*Stipa thurberiana* Piper), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria cristata* auct. p.p. non Pers), and squirreltail (*Sitanion hystrix* (Nutt.)) are the co-dominant perennial bunchgrasses on the study site. Six plots were located at the NGBER.

Baker Pass

Baker Pass is located in southeastern Oregon about 80 km south of Burns, OR. Average precipitation at Baker Pass was estimated to range between 300 and 360 mm annually (Natural Resource Conservation Service 1998). Elevation ranges from 1,350 to 1,450 m above sea level. Slopes averaged 13° and aspect is north facing. Soil surface texture is loamy. Incidental radiation averages $0.83 \text{ cm}^{-2} \text{ yr}^{-1}$. Wyoming big sagebrush is the dominant shrub, and on three plots bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) and on one plot Idaho fescue is the dominant perennial bunchgrass.

Experimental Design and Statistical Analysis

A randomized block design was used to test the influence of Wyoming big sagebrush on microsite and herbaceous vegetation. Six $80 \times 50 \text{ m}$ (0.4 ha) blocks

were randomly located across a 53 ha Wyoming big sagebrush community at the NGBER. Treatments were designated by zonal location: under (subcanopy) and between (interspace) sagebrush canopies. Analysis of variance (ANOVA) was used to determine zonal differences in herbaceous vegetation and microsites (Table 5.1).

To examine if zonal differences in vegetation cover and density were consistent among Wyoming big sagebrush sites, four additional plots with more northerly exposures were evaluated at Baker Pass. ANOVA tests were used to determine if zonal differences in vegetation cover and density existed at Baker Pass (Table 5.2). Fisher LSD was used to test for differences in means. Means were considered significantly different if the p-value was less than 0.05.

Measurements

Micro-environment

Micro-environmental variables in subcanopy and interspace zones were measured at the NGBER site. Soil and air temperature, relative humidity, and photosynthetically active radiation (PAR) measurements were recorded every three hours starting at midnight of each day from April through early November. Soil temperature (°C) was measured with Hobo 4-Channel temperature units at a depth of 4 cm below the soil surface. Two Hobo 4-Channel temperature units were placed in each block. Two channels from each unit recorded temperature for each zone. Air temperature (°C) and relative humidity (%) were measured at 30 cm above the soil surface with Hobo RH

and TEMP units. Six Hobo RH and TEMP units were placed in each zone per block. PAR ($\mu\text{mol}/\text{m}^2/\text{sec}$) was measured with Hobo Microstations with smart sensors placed 10 cm above the soil surface. Four smart sensors measured PAR in each zone.

Soil

In both zones of each treatment replication, five soil cores from 0-15 cm and 15-30 cm depths were collected at two-week intervals during the growing season to measure soil water content. Water content of the soil was determined gravimetrically. Soil pH, total nitrogen, total carbon, and organic matter in the upper 15 cm of the soil profile were determined from five soil samples, collected in July, from each zone per block. Total carbon and total nitrogen were determined using a LECO CN 2000. Soil samples were not calcareous. Organic matter was estimated using an amended Rather method (Nelson and Sommers 1982). Soil nitrate (NO_3^-) and ammonium (NH_4^+) content were measured by collecting two samples from each zone in each block every month during the growing season. Each sample consisted of five compiled 0-15 cm soil cores. Nitrogen fractions were extracted using 2N KCl solution. The extracted solution was analyzed for NO_3^- and NH_4^+ content by Oregon State University's Central Analytical Lab. Soil surface texture (0-15 cm) was determined from five samples from each zone in every block using the hydrometer method (Gee and Bauder 1986).

Table 5.1. ANOVA models used to test for differences ($p < 0.05$) between zones at the NGBER.

Variables	Degrees of Freedom
Soil Water Content	
Block	5
Sampling Date	7
Treatment	1
Treatment:Date	7
Residuals	171
Soil Inorganic Nitrogen	
Block	5
Sampling Date	7
Treatment	1
Treatment:Date	7
Residuals	75
Soil C, N, OM, pH, texture	
Block	5
Year	1
Treatment	1
Treatment: Year	1
Residuals	15
PAR, RH, Temp	
Block	5
Sampling Date	390
Treatment	1
Treatment:Date	390
Residuals	1553
Herb. Biomass Production	
Block	5
Treatment	1
Residuals	5
Herb. Cover & Density	
Block	5
Year	1
Treatment	1
Treatment: Year	1
Residuals	15
Photosynthetic Rate & Stomatal Conductance	
Block	5
Sampling Date	10
Treatment	1
Treatment:Date	10
Residuals	105
C and N isotopes	
Block	5
Year	1
Treatment	1
Treatment: Year	1
Residuals	15

Table 5.2. ANOVA models used to test for differences ($p < 0.05$) between zones at the Baker Pass.

Variables	Degrees of Freedom	
Herb. Cover & Density	Block	3
	Year	1
	Treatment	1
	Treatment: Year	1
	Residuals	9

Herbaceous

Herbaceous cover by species, functional group biomass, and perennial species densities were measured in 30 subcanopy and adjacent interspace zones using 0.4 m² frames (two side by side 0.2 m² frames) (Figure 5.1). Subcanopy zones were randomly selected and adjacent interspaces were located two meters to the east. Density, cover, and composition were measured in 2003 and 2004. Biomass was measured in 2004. Herbaceous vegetation was clipped, oven-dried, separated into current year's and previous years' growth, and weighed to determine biomass production.

Thurber's needlegrass was used to determine differences in the availability of resources to herbaceous vegetation in the two zones at the NGBER. Photosynthetic rate and stomatal conductance were determined for three Thurber's needlegrass plants from each zone per block every two weeks during the growing season using a Li-Cor 6200 Portable Photosynthesis Unit and a Li-Cor 2100 Leaf Area Meter. Carbon isotope ratio, nitrogen isotope ratio, carbon content, and nitrogen content were measured from five Thurber's needlegrass individuals from each zone in every block.

Samples were collected in late June, oven-dried, and then ground to pass through a 40 mm screen. Ground samples were sent to the University of Utah Stable Isotope Research Facility for Environmental Research for analysis. In a review of several studies, Evans (2001) showed that the heavier nitrogen-15 isotope discrimination increased with greater nitrogen availability. The nitrogen isotope ratio was used to compare nitrogen availability between zones. Carbon-13 is discriminated against in C3 plants, allowing for a time-integrated estimate of water-use efficiency (Farquhar et al. 1989, Ehleringer et al. 1993), and discrimination has been reported to increase with greater water availability (Toft et al. 1989). The carbon isotope ratio was used to compare water availability between zones.

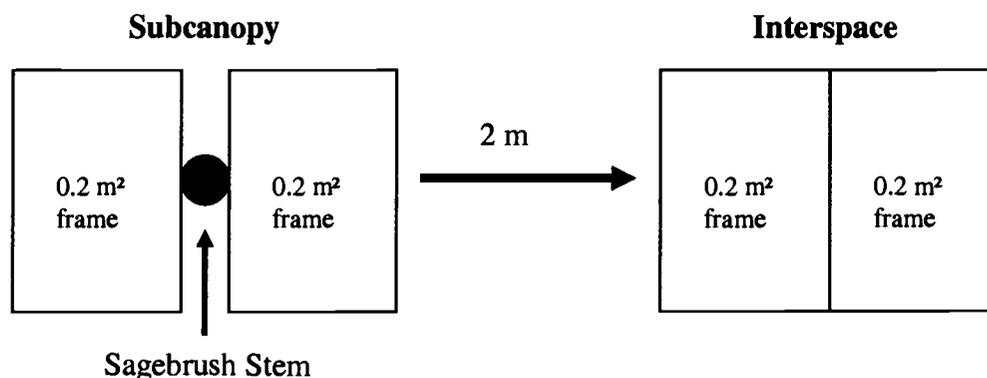


Figure 5.1. Placement of frames in subcanopy and interspace zones. The two 0.2 m² frames were placed next to one another. For subcanopy measurements, the shrub's stem divided the two 0.2 m² frames. The stem was centered on the long axis of the frames. Not drawn to scale.

Results

Micro-environment

Maximum and minimum daily soil temperatures varied by date and zone ($p < 0.05$). The interaction of date and zone was significant for both maximum and minimum daily soil temperatures ($p < 0.05$). Subcanopy maximum daily soil temperature averaged 14.7°C less than the interspace from April through October ($p < 0.0001$) (Figure 5.2) (Table 5.3). Subcanopy minimum daily soil temperature was 2.2°C warmer than the interspace ($p < 0.0001$) (Table 5.3).

Maximum daily air temperature was not different between the zones ($p = 0.0605$), but minimum daily air temperature was slightly cooler in the interspace than the subcanopy ($p < 0.0001$) (Table 5.3). Maximum and minimum daily air temperatures varied by date ($p < 0.05$). Average daily PAR in the subcanopy was $297 \mu\text{mol}/\text{m}^2/\text{sec}$ less than the interspace from April through October ($p < 0.0001$). Average daily PAR also varied by date, and the interaction between date and zone was also significant ($p < 0.05$). Maximum and minimum relative humidity varied by date and zone ($p < 0.05$) and were slightly less in the subcanopy than interspace ($p < 0.0001$).

Soil Characteristics

Percent clay, silt, and sand were not different between the subcanopy and interspace zones or years ($p > 0.05$). Soil organic matter, pH, total C, and total N were

greater in the subcanopy than the interspace zone ($p < 0.05$) (Table 5.4), but did not differ among years ($p > 0.05$). Though NO_3^- and NH_4^+ varied by sample date ($p < 0.0001$) and between zones on a few select dates (Fig. 5.3), they were not different between zones across the growing season ($p > 0.05$) (Table 5.4).

Table 5.3. Soil and air temperature, PAR, and relative humidity differences between subcanopy and interspace zones.

Daily Characteristic	Subcanopy (mean)	Interspace (mean)	p-value for difference of means	Standard Error for difference of means
Max. Soil Temperature (°C)	21.4	35.9	< 0.0001 *	0.0771
Min. Soil Temperature (°C)	10.4	8.3	< 0.0001 *	0.0480
Max. Air Temperature (°C)	25.5	25.2	0.0605	0.0650
Min. Air Temperature (°C)	5.7	5.6	< 0.0001 *	0.0198
Average PAR ($\mu\text{mol}/\text{m}^2/\text{sec}$)	221	518	< 0.0001 *	2.6900
Max. Relative Humidity (%)	75.4	76.8	< 0.0001 *	0.1020
Min. Relative Humidity (%)	21.4	22.4	< 0.0001 *	0.0924

Asterisk (*) indicates significant difference in zonal means ($p < 0.05$).

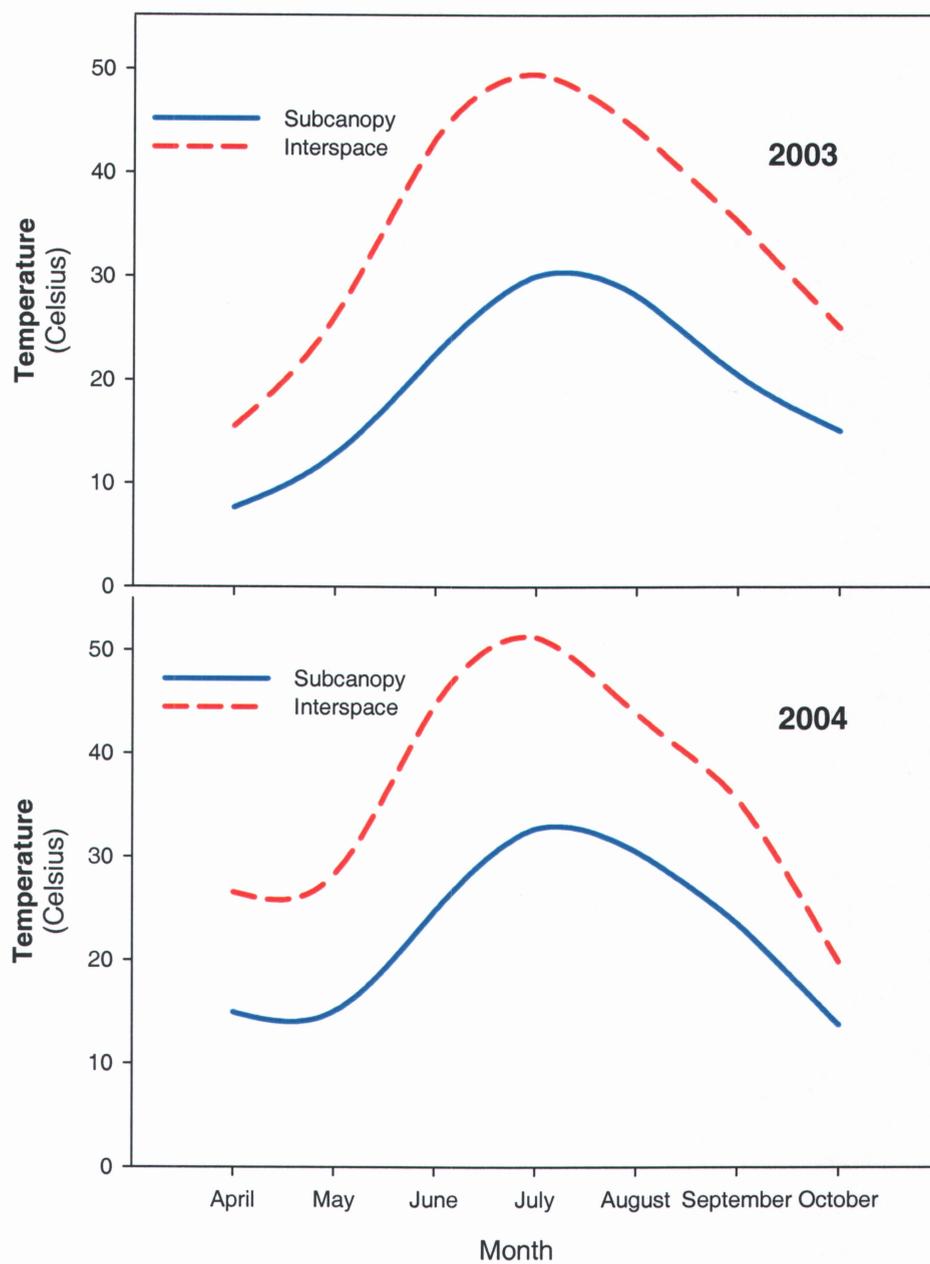


Figure 5.2. Subcanopy and interspace zone maximum daily soil temperatures at 4 cm depth.

Table 5.4. Subcanopy and interspace soil characteristics (0-15 cm) at NGBER.

Soil Parameter	Subcanopy (mean)	Interspace (mean)	p-value for difference of means	Standard Error for difference of means
Clay (%)	7.2	7.6	0.4120	0.5001
Silt (%)	23.1	24.3	0.5501	1.7962
Sand (%)	69.7	68.1	0.4660	2.0301
pH	7.1	6.9	0.0005 *	0.0387
Organic Matter (%)	1.4	1.2	0.0236 *	0.0727
Total Carbon (%)	0.99	0.76	0.0008 *	0.0536
Total Nitrogen (%)	0.08	0.07	0.0058 *	0.0039
NO ₃ (ppm)	0.12	0.14	0.1102	0.0141
NH ₄ (ppm)	1.04	1.06	0.4900	0.0398

Asterisk (*) indicates significant difference in zonal means ($p < 0.05$).

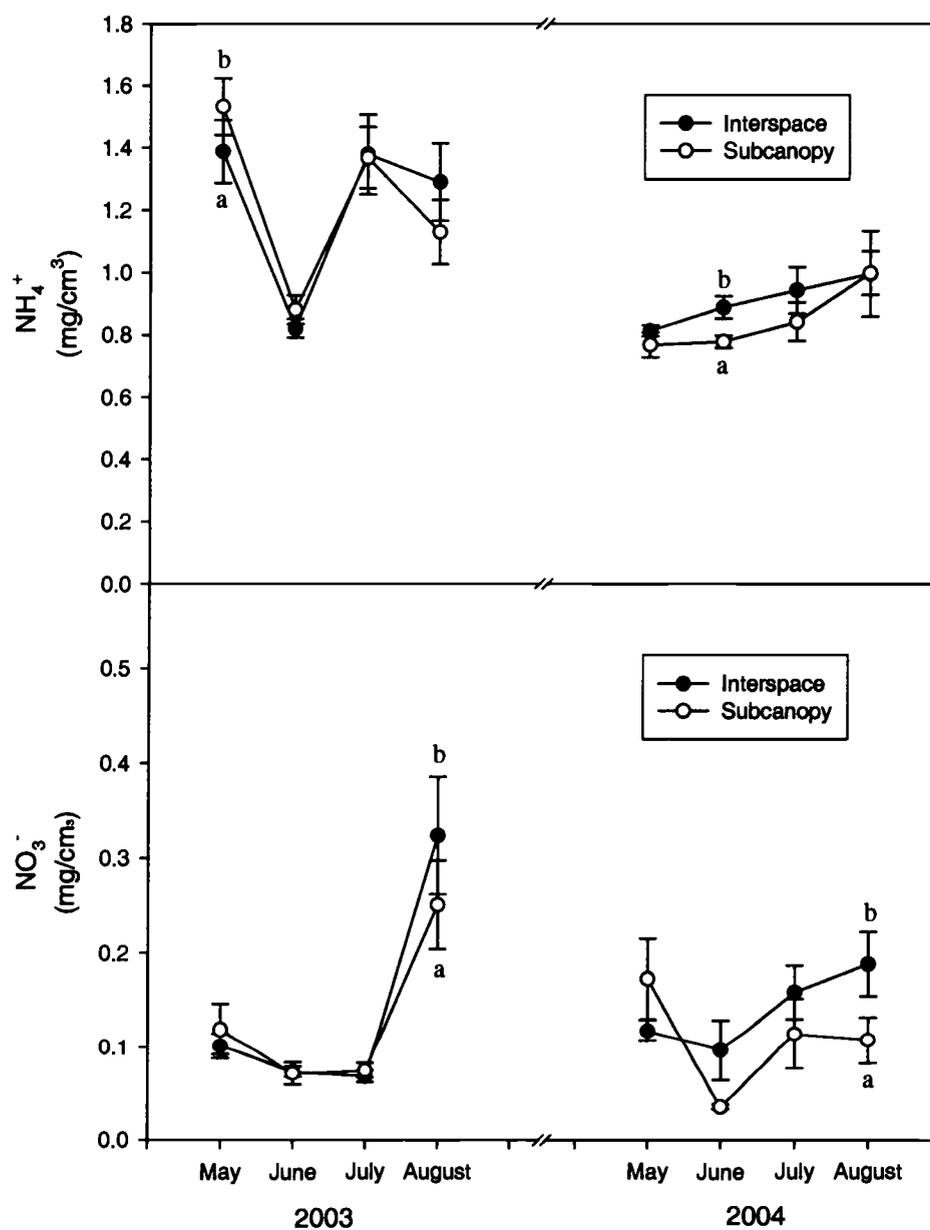


Figure 5.3. Soil nitrate and ammonium content (mean \pm 1 standard error) in the subcanopy and interspace zone. Different lower case letters indicate when there is a difference between zones at that date ($p < 0.05$).

Soil water content (0-15 cm) varied by sampling date and zone ($p < 0.05$). The subcanopy had greater soil water content (0-15 cm) than the interspace during the growing season ($p < 0.0001$, S.E. = 0.1425; mean = 8.4 and 7.4%, respectively). However, the subcanopy and interspace were not always different on individual sampling dates (Figure 5.4 A). Soil water content (15-30 cm) varied by sampling date ($p < 0.0001$), but was not significantly different among zones during the growing season ($p = 0.0628$). However, soil water content (15-30 cm) was infrequently different between zones on individual sampling dates (Figure 5.4 B).

Vegetation

Physiological response of Thurber's needlegrass to zonal location

Thurber's needlegrass carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$) was more negative when grown in the subcanopy than interspace zone ($p = 0.0022$) (Table 5.5). Total percent carbon and nitrogen, and nitrogen isotope ratio ($^{15}\text{N}/^{14}\text{N}$) of Thurber's needlegrass were not different between zones ($p > 0.05$) (Table 5.5). Total percent carbon and nitrogen isotope ratio varied by year ($p = 0.0159$ and 0.0011 , respectively).

Photosynthetic rates of Thurber's needlegrass did not differ between zones on most dates sampled (Fig. 5.5). However, over the growing season, photosynthetic rates averaged $1.06 \mu\text{mol m}^{-2} \text{s}^{-1}$ greater in the interspace than the subcanopy ($p = 0.0265$, S.E. = 0.4710). Photosynthetic rates varied by sampling date because it generally declined over the growing season ($p < 0.0001$) (Fig. 5.5). Stomatal conductance did not vary by zone ($p = 0.8242$), but did vary by date ($p < 0.0001$).

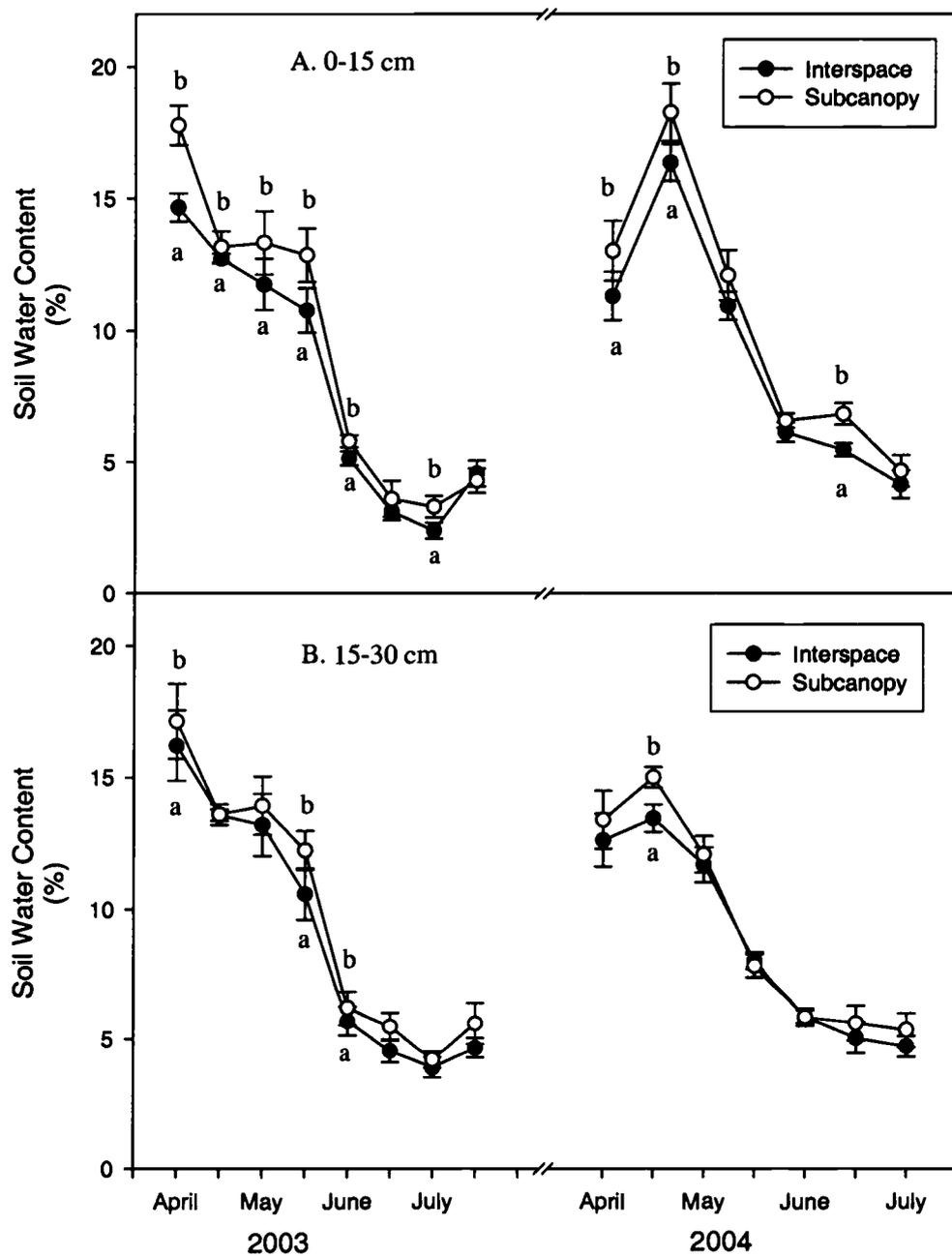


Figure 5.4. Soil water content (mean \pm 1 standard error) in the subcanopy and interspace zones at 0-15 cm and 15-30 cm depths. Different lower case letters indicate when there is a difference between zones at that date ($p < 0.05$).

Table 5.5. Zonal carbon and nitrogen characteristics of Thurber's needlegrass.

Characteristic	Subcanopy (mean)	Interspace (mean)	p-value for difference of means	Standard Error for difference of means
$^{13}\text{C}/^{12}\text{C}$ ratio (‰)	-26.6	-26.1	0.0022 *	0.1339
$^{15}\text{N}/^{14}\text{N}$ ratio (‰)	2.6	2.8	0.5474	0.3598
Total Carbon (%)	42.0	42.1	0.8479	0.2816
Total Nitrogen (%)	1.3	1.2	0.0667	0.0418

Asterisk (*) indicates significant difference in zonal means ($p < 0.05$).

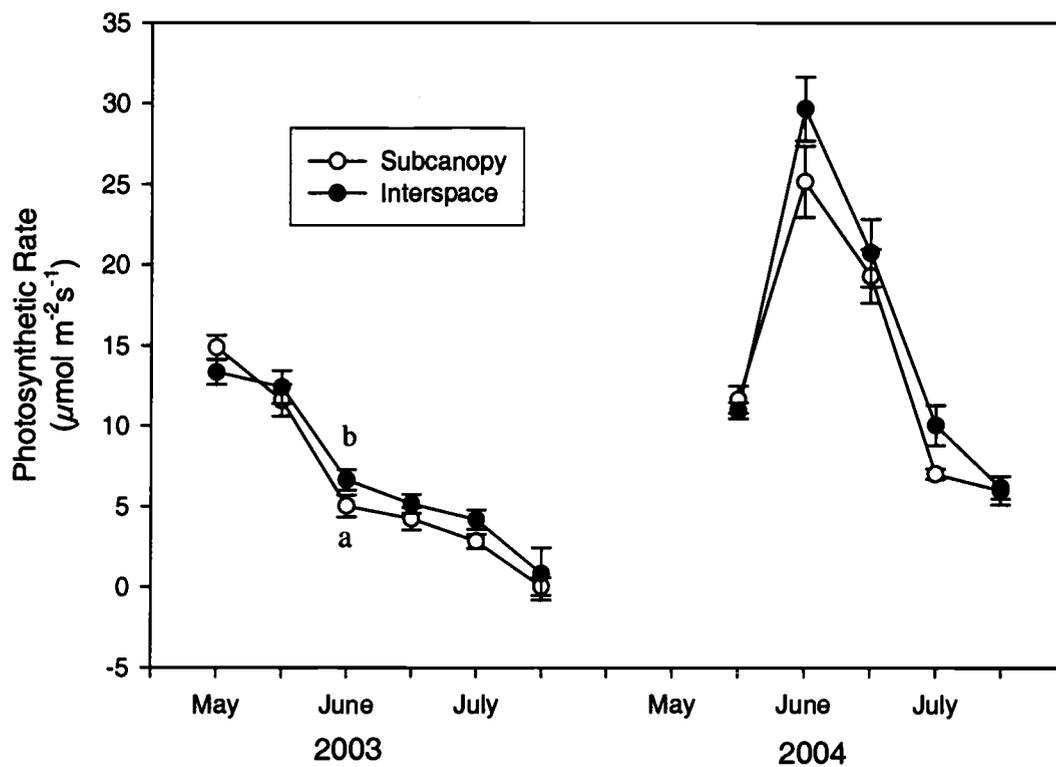


Figure 5.5. Photosynthetic rates (mean \pm 1 standard error) for Thurber's needlegrass in subcanopy and interspace zones. Different lower case letters indicate a difference in photosynthetic rates between zones on that date.

Cover

NGBER Site

Zonal location influenced herbaceous cover values (Fig. 5.6). The subcanopy zone had greater tall tussock perennial grass, Sandberg bluegrass, annual grass, total herbaceous, litter, and moss cover and less bare ground than the interspace ($p < 0.05$).

Moss, tall tussock perennial grass, Sandberg bluegrass, and total herbaceous cover values were different between years ($p < 0.05$). Tall tussock perennial grass, Sandberg bluegrass, moss, and total herbaceous cover were greater in 2003 than 2004 ($p < 0.05$), but the interaction of treatment and year was not significant ($p > 0.05$). All other functional groups did not differ between years ($p > 0.05$). Idaho fescue, prairie junegrass, and squirreltail cover values were greater in the subcanopy than the interspace ($p < 0.05$) (Fig. 5.7). Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), needle-and-thread (*Stipa comata* Trin. & Rupr.), and Thurber's needlegrass cover values did not differ between zones ($p > 0.05$) (Fig. 5.7).

Baker Pass Sites

Few zonal differences in cover were measured at Baker Pass (Fig. 5.8). Litter and moss cover were greater in the subcanopy compared to the interspace zone ($p < 0.05$). Bare ground was less in the subcanopy than interspace ($p < 0.05$). Perennial forb cover was greater and tall tussock perennial grass cover was lower in 2004 compared to 2003 ($p < 0.05$), but the interaction of treatment and year was not significant ($p > 0.05$). Except for squirreltail ($p = 0.0383$, S.E. = 0.2226), tall tussock perennial grass species cover values did not vary by zone ($p > 0.05$) (Fig. 5.9). Squirreltail cover averaged 1.21% and 0.67% in the subcanopy and interspace, respectively. None of the tall tussock perennial grass species cover values varied by year ($p > 0.05$).

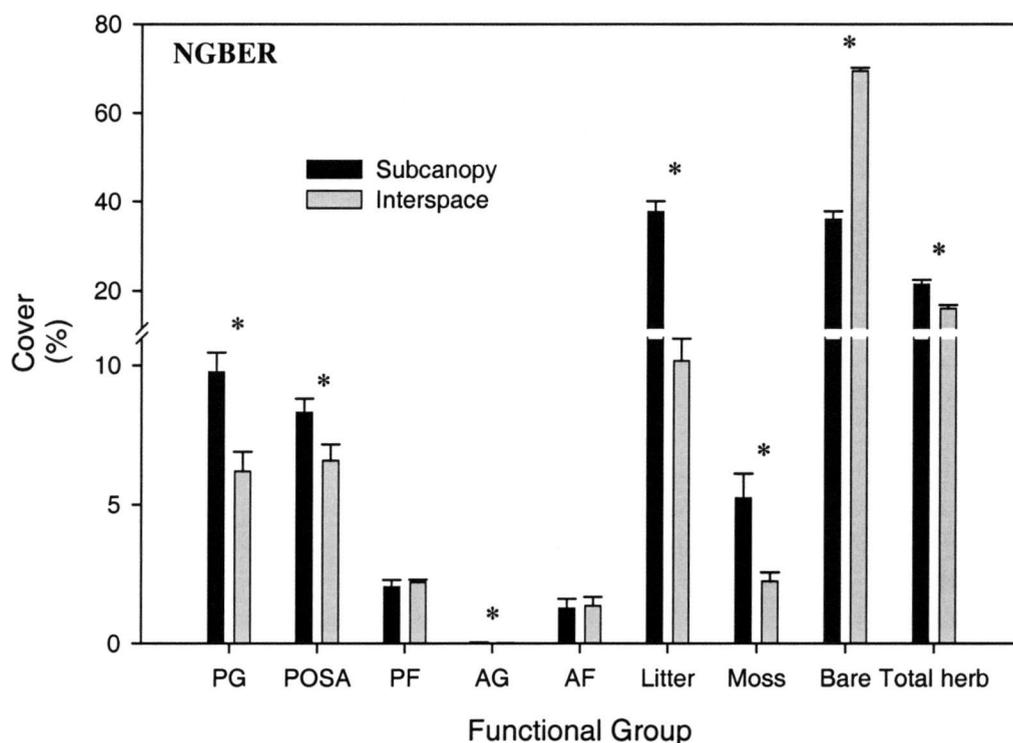


Figure 5.6. Zonal functional group cover values with standard error bars at NGBER. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). PG = Tall tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, AG = Annual grass, AF = Annual forb, Bare = Bare ground, and Total herb = Total herbaceous.

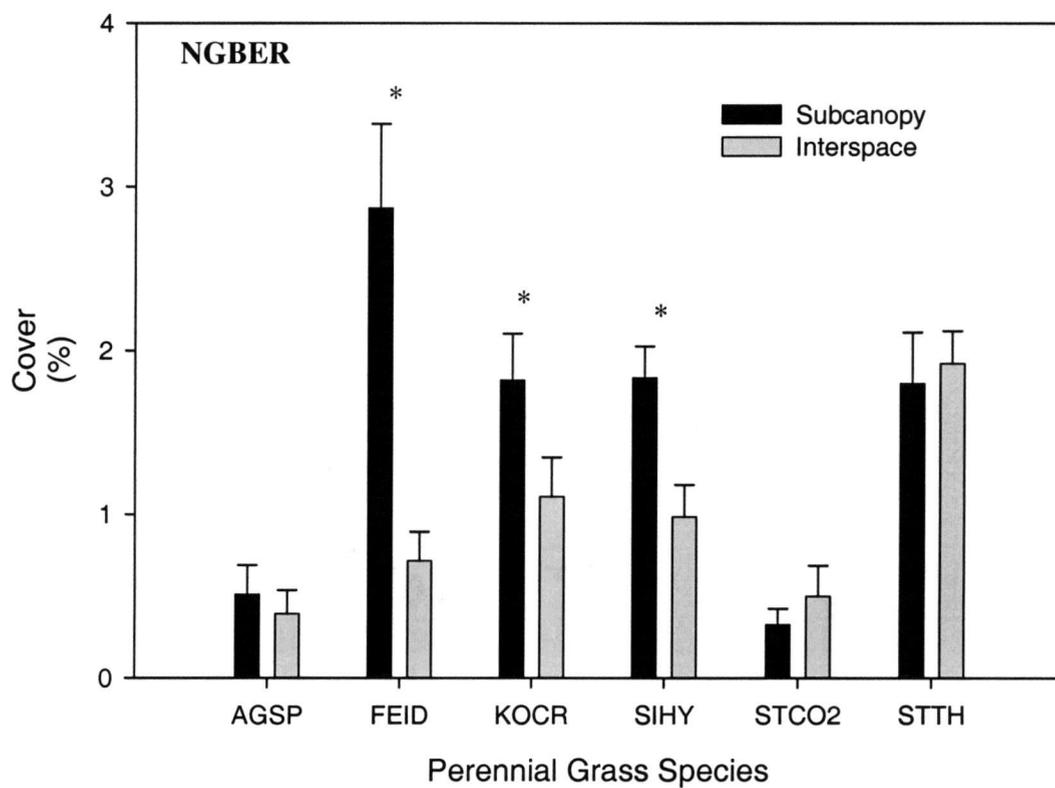


Figure 5.7. Zonal tall tussock perennial grass species cover values with standard error bars at NGBER. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). AGSP = bluebunch wheatgrass, FEID = Idaho fescue, KOGR = prairie junegrass, SIHY = squirreltail, STCO2 = needle-and-thread, and STTH = Thurber's needlegrass.

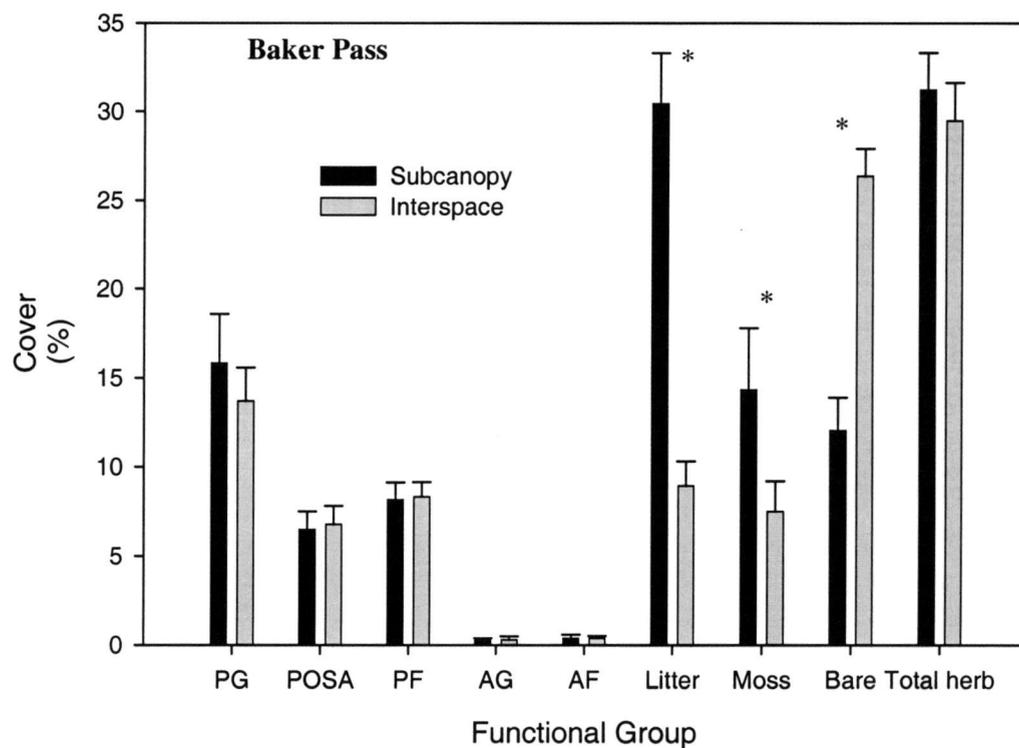


Figure 5.8. Subcanopy and interspace cover values with standard error bars at Baker Pass. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). PG = Tall Tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, AG = Annual grass, AF = Annual forb, Bare = Bare ground, and Total herb = Total herbaceous.

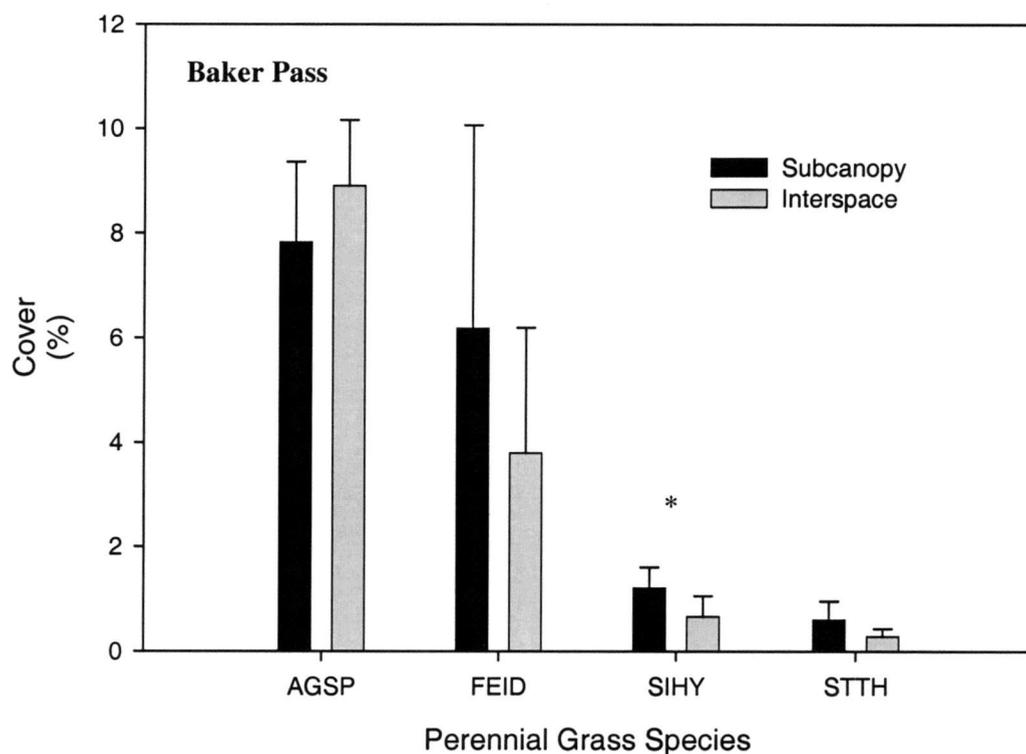


Figure 5.9. Zonal tall tussock perennial grass species cover values with standard error bars at Baker Pass. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). AGSP = bluebunch wheatgrass, FEID = Idaho fescue, SIHY = squirreltail, and STTH = Thurber's needlegrass.

Density

NGBER Plots

The subcanopy had greater density of Sandberg bluegrass, tall tussock perennial grass, and total perennial species than the interspace ($p < 0.05$) (Fig. 5.10). Perennial forb density did not exhibit zonal differences ($p > 0.05$). Tall tussock perennial grass, Sandberg bluegrass, and total perennial species densities were greater in 2003 than 2004 ($p < 0.05$), but the interaction of year and treatment was not significant ($p >$

0.05). Idaho fescue, prairie junegrass, and squirreltail densities were greater in the subcanopy than interspace ($p < 0.05$) (Figure 5.11), but did not vary by year ($p > 0.05$). Bluebunch wheatgrass, needle-and-thread, and Thurber's needlegrass densities did not differ among zones or years ($p > 0.05$).

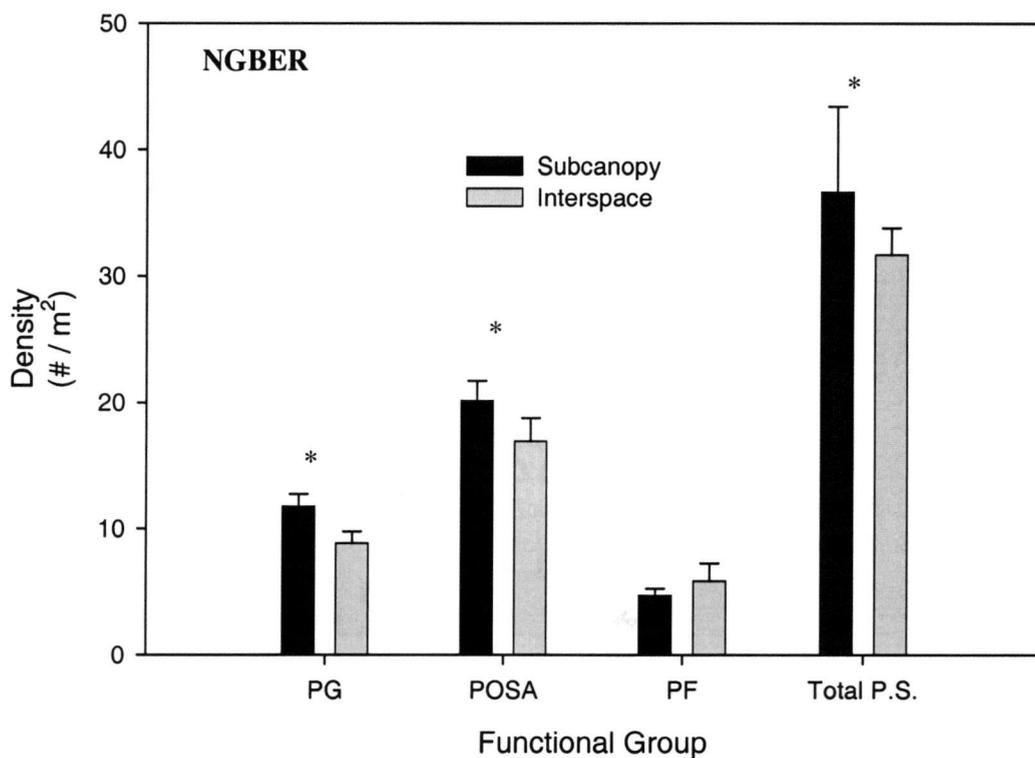


Figure 5.10. Zonal perennial functional group densities with standard error bars at the NGBER. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). PG = Tall tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, and Total P.S. = Total perennial species.

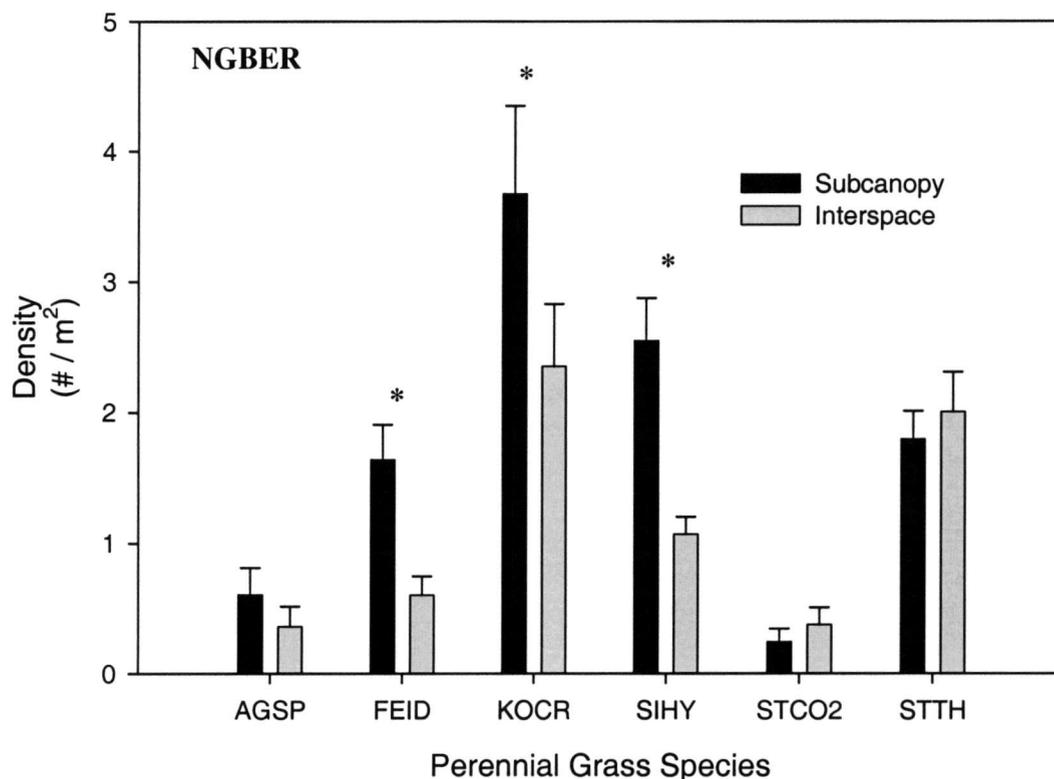


Figure 5.11. Zonal tall tussock perennial bunchgrass species densities with standard error bars at the NGBER. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). AGSP = bluebunch wheatgrass, FEID = Idaho fescue, KOCCR = prairie junegrass, SIHY = squirreltail, STCO2 = needle-and-thread, and STTH = Thurber's needlegrass.

Baker Pass Plots

Sandberg bluegrass and bluebunch wheatgrass densities differed between zones at Baker Pass. Sandberg bluegrass averaged 23 and 29 plants per m² in the subcanopy and interspace, respectively ($p = 0.0068$, S.E. = 1.744). Bluebunch wheatgrass density was 4.1 and 7.5 plants per m² in the subcanopy and interspace, respectively ($p = 0.0354$, S.E. 2.494). None of the other perennial functional groups (Fig. 5.12) or tall

tussock perennial grass species densities (Fig. 5.13) varied between zones ($p > 0.05$). Perennial forb density was greater in 2004 than 2003 ($p = 0.0004$), while tall tussock perennial grass density was greater in 2003 than 2004 ($p = 0.0449$). The interaction of year and treatment were not significant ($p > 0.05$).

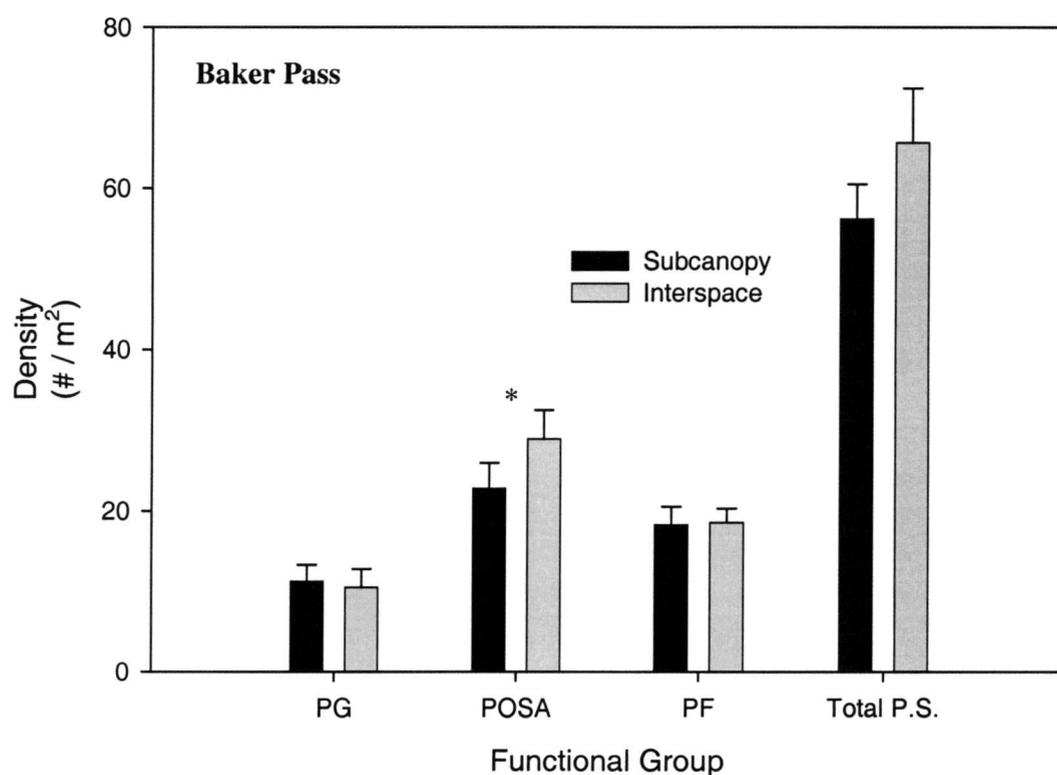


Figure 5.12. Zonal perennial functional group densities with standard error bars at Baker Pass. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). PG = Tall tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, and Total P.S. = Total perennial species.

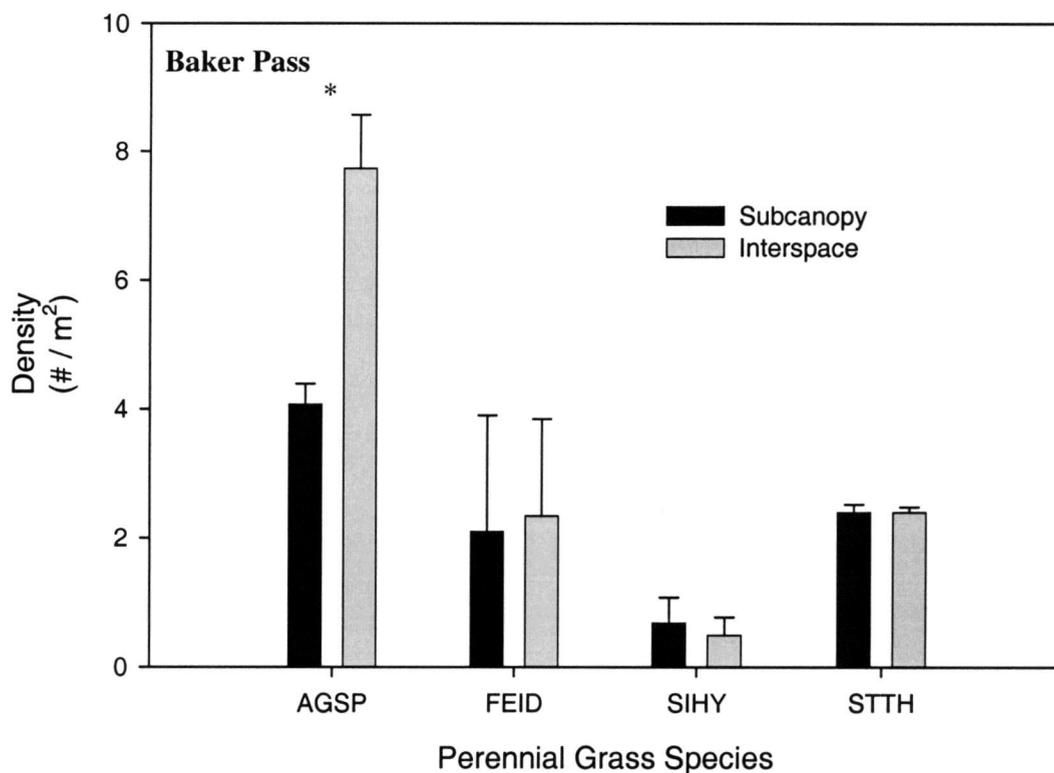


Figure 5.13. Zonal tall tussock perennial bunchgrass species densities with standard error bars at Baker Pass. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). AGSP = bluebunch wheatgrass, FEID = Idaho fescue, SIHY = squirreltail, and STTH = Thurber's needlegrass.

Biomass Production

Tall tussock perennial grass and total herbaceous biomass production were greater in the subcanopy than the interspace ($p = 0.0351$ and 0.0330 , respectively) (Fig. 5.14). Annual forb biomass production was greater in the interspace than the subcanopy ($p = 0.0481$).

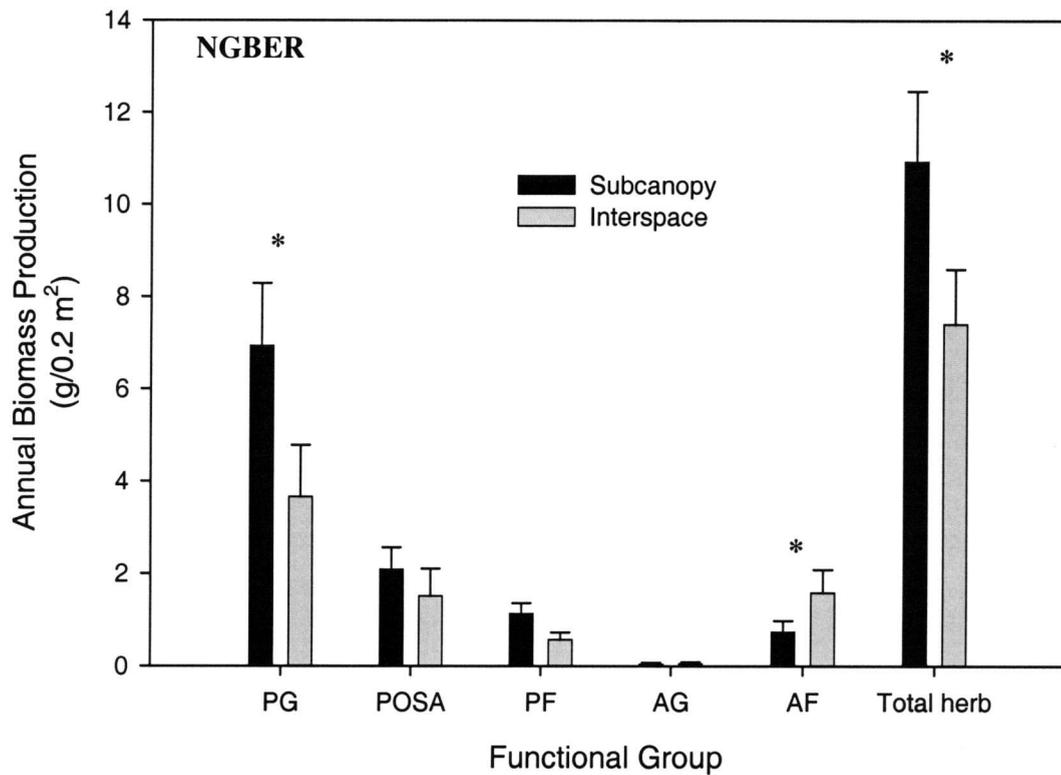


Figure 5.14. Subcanopy and interspace functional group annual biomass production with standard error bars at the NGBER in 2004. Asterisk (*) indicates significant differences in zonal means ($p < 0.05$). PG = Tall tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, AG = Annual grass, AF = Annual forb, and Total herb = Total herbaceous.

Discussion

We accepted the first hypothesis that Wyoming big sagebrush creates differing subcanopy and interspace micro-environments at the NGBER. Our results agreed with other studies demonstrating moderated soil temperatures (Pierson and Wight

1991), greater soil water content (Wight et al. 1992, Chambers 2000), and higher C and N (Charley and West 1975, Doescher et al. 1984, and Burke et al. 1987) beneath sagebrush canopies compared to interspaces. These factors appear to explain the zonal differences measured for herbaceous vegetation at the NGBER site. Although soil pH, relative humidity, minimum soil temperature, and air temperatures differed between zones, differences were small and likely biologically insignificant. Greater herbaceous cover, perennial grass densities, and total herbage production in the subcanopy suggested that this zone provides a more favorable microsite for herbaceous growth than the interspace. Physiological response of Thurber's needlegrass demonstrated that sagebrush can create zonal differences in the availability and use of resources, thus the second hypothesis was accepted. Greater discrimination by Thurber's needlegrass against ^{13}C when growing in the subcanopy zone indicated that water was more available to Thurber's needlegrass growing in the subcanopy than interspace. However, photosynthetic rates were lower in Thurber's needlegrass growing in the subcanopy than interspace zone indicating zonal differences in resource availability. The lower photosynthetic rates in the subcanopy zone were likely the result of competition or interference limiting the availability of resources other than water.

In contrast to the NGBER site, the Baker Pass site had fewer measurable differences in zonal vegetation characteristics. This suggests that the influence of microsite on the spatial distribution of herbaceous vegetation in sagebrush

communities is site dependent. Doescher et al. (1984) found the spatial distribution of soil nutrients to be site dependent in big sagebrush communities. Microsite (environmental and soil resources) characteristics were not measured at Baker Pass, and it is possible that zonal differences for these variables were not as pronounced at this location compared to the NGBER site. However, the macro-environment at Baker Pass is less harsh for plant growth than the NGBER. At Baker Pass, aspect is north facing and steep; thus, the site is less exposed (lower incident radiation) than the NGBER site. Lower incidental radiation and/or other unmeasured site characteristics may be responsible for the lack of zonal differences in herbaceous composition at Baker Pass. For example, at the NGBER site, Idaho fescue and Sandberg bluegrass mainly occupied subcanopy zones, while at the Baker Pass site no zonal preference was measured or, in the case of Sandberg bluegrass density, the relationship was reversed. The strong zonal vegetation differences at the NGBER site resulted in acceptance of the third hypothesis for that particular site, but not for the Baker Pass site.

As well as site dependency, measurements at the NGBER site suggest that zonal herbaceous distribution may also be species dependent. Cover and density of Idaho fescue, prairie junegrass, and squirreltail were greater under the sagebrush canopy than the interspace, while other herbaceous species exhibited no zonal preference. Other authors have also found differing species response to zonal location. Singleleaf pinyon establish preferentially under big sagebrush canopies, while ponderosa pine

(*Pinus ponderosa* P. & C. Lawson) establish best in interspaces (Callaway et al. 1996). In contrast to our study, Hazlett and Hoffman (1975) and Eckert et al. (1986) found that forbs preferentially established under sagebrush canopies, while grass cover was greater in the interspaces. The lack of zonal differences in forbs in our study may be a reflection of year effect. Both study years were below average for precipitation and were characterized by dry springs. At the NGBER and elsewhere in the Great Basin, forb production is correlated to spring precipitation (Passey et al. 1982, Sneva 1982, Bates et al. 2004). In the Eckert et al. (1986) study, their study years coincided with above average precipitation.

Conclusions

Wyoming big sagebrush appears to modify microsite and resource availability within stands. Sagebrush is an important component contributing to the heterogeneity of herbaceous vegetation within a community. However, by comparing zonal herbaceous characteristics from two different Wyoming big sagebrush communities, we found sagebrush's influence on herbaceous spatial heterogeneity to be site dependent.

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CHAPTER 6

**THE EFFECTS OF BURNING WYOMING BIG SAGEBRUSH ON
COMMUNITY RESOURCE CAPTURE AND USE**

Kirk W. Davies, Jonathan D. Bates, Richard F. Miller

THE EFFECTS OF BURNING WYOMING BIG SAGEBRUSH ON COMMUNITY RESOURCE CAPTURE AND USE

Abstract

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh) plant communities of the Intermountain West have been greatly reduced from their historic range as a result of wildfire, agronomic practices, and brush control treatments. The consequences of sagebrush loss to community resource capture and use has not been well quantified. This study evaluated the effects of Wyoming big sagebrush removal by burning on resource capture and use. Treatments were sagebrush removed with burning (burned) and sagebrush present (control). Biomass production, vegetation cover, perennial herbaceous vegetation diversity, soil water content, soil inorganic nitrogen (NO_3^- , NH_4^+), total soil nitrogen (N), total soil carbon (C), soil organic matter (OM), microtopography, and Thurber's needlegrass (*Stipa thurberiana* Piper) photosynthetic rates were compared between treatments. In the first two post-burn years (2003 and 2004), total biomass production was 2.3 and 1.2 times greater, respectively, in the control than the burned treatment, indicating resources were not fully exploited in the burn treatment. Greater herbaceous production and photosynthetic rates in the burned treatment indicated resources were more available to herbaceous vegetation in the burned than control treatment. However, soil water content in spring was greater in the control than burned treatment

in both years of the study, which indicated reduced precipitation capture after sagebrush was removed. Microtopography decreased the first year, but did not change significantly in the second year after burning. Removal of Wyoming big sagebrush decreases community resource capture and use the first two years after fire.

Removing sagebrush with fire opens the site up to herbaceous colonization. The study area was relatively weed free, and herbaceous perennial mortality was low in response to the burn; thus, the threat of weed invasion was low.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh)¹ is the most extensive subspecies of big sagebrush (*Artemisia tridentata* Nutt.) in the western United States (Küchler 1970, Miller et al. 1994, West and Young 2000). The Wyoming big sagebrush alliance is considered the least resilient and most susceptible of the big sagebrush complex to invasion by exotic weeds (Miller and Eddleman 2000). Large areas of Wyoming big sagebrush have converted to cheatgrass (*Bromus tectorum* L.) dominated annual grasslands in the Intermountain West. Further reductions in the alliance are the result of brush control programs, conversion to croplands, and urbanization (Young et al. 1981, Miller and Eddleman 2000).

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press. Seattle, WA. 730 p.

Fire was a natural disturbance within sagebrush communities that shifted communities from shrub to grass dominance (Wright and Bailey 1982). There has been a large volume of research regarding the effects of wildfire and prescribed burning on sagebrush communities in the western United States (Blaisdell 1953, Wright and Klemmedson 1965, Harniss and Murray 1973, Peek et al. 1979, Humphrey 1984, West and Hassan 1985, Wambolt et al. 2001, and West and Yorks 2002). Previous research has primarily focused on increasing herbage production and evaluating the effects on wildlife habitat. The implications of removing sagebrush with fire on community resource capture and use remains largely unexplored. The effects of burning sagebrush communities on soils have also received limited attention. Blank et al. (1994) reported decreased nitrate and orthophosphate, and increased acetate, formate, oxalate, glycolate, organic acids, and sulfate following fire in a sagebrush community, but did not investigate alterations to resource capture or use. Their study site was dominated by cheatgrass (*Bromus tectorum* L.); thus, extrapolating their results to burning in an intact, late seral Wyoming big sagebrush community may not be appropriate.

In this study, we explored the role of Wyoming big sagebrush in the capture and use of water and energy (biomass). Resource capture and use have significant implications for community stability. The susceptibility of a plant community to weed invasion increases with inefficiencies in resource use (Sheley et al. 1999b). Fire and other disturbances in natural systems can result in inefficiencies in resource capture

and use. We hypothesized that the removal of Wyoming big sagebrush with burning decreases community resource capture and use in the first two years after fire.

Methods

Site Description

The study was conducted at the Northern Great Basin Experimental Range (NGBER) in southeastern Oregon (43.4711 Lat., 119.6916 Long.) about 56 km west of Burns, OR. The NGBER receives on average 300 mm of precipitation annually (EOARC data file). The majority of precipitation comes in the winter and spring. Elevation is approximately 1,400 m above sea level and topography is flat (slopes < 2°) at the study site. Soils at the study site are a complex of Haploxerolls, Agrixerolls, Durixerolls, and Durargids (Lentz and Simonson 1986). Wyoming big sagebrush is the dominant shrub, and Thurber's needlegrass (*Stipa thurberiana* Piper), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria cristata* auct. p.p. non Pers), and squirreltail (*Sitanion hystrix* (Nutt.)) are the co-dominant perennial bunchgrasses. Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & J.G. Sm.) is also very common at the site. Common perennial forbs include hawksbeard (*Crepis* sp. L.), curve-pod milkvetch (*Astragalus curvicaarpus* (Heller) J.F. Macbr.), tailcup lupine

(*Lupinus caudatus* Kellogg), common yarrow (*Achillea millefolium* L.), and long-leaved phlox (*Phlox longifolia* Nutt.).

Experimental Design

A randomized block design was used to investigate the effects of removing Wyoming big sagebrush with burning on the measured response variables. Six blocks were randomly selected across a 53 ha rangeland. Each block consisted of two 50 X 80 m (0.4 ha) plots randomly assigned a burn or unburned (control) treatment. This resulted in six control and six burned plots. The burn treatment was applied in October 2002 using a gel-fuel terra torch.

Vegetation Sampling

Biomass production was the sum of the current year above-ground shrub and herbaceous production. Herbaceous biomass was determined in late June of each year by clipping, oven drying, and then weighing the current year's growth from twenty-five randomly located 1 m² frames per plot.

Sagebrush biomass (gm) production was determined by modifying an equation developed by Rittenhouse and Sneva (1977) on the NGBER. Seventy-five Wyoming big sagebrush plants were randomly selected for measurement in July prior to ephemeral leaf drop. Sagebrush volume was determined by measuring crown width

and height prior to harvest. Harvested sagebrush was dried and current year's growth (leaves and reproductive stems) was removed and weighed to determine annual biomass production. Equations were modified each year to correlate canopy volume (cm^3) with annual production; they were:

2003 Sagebrush Biomass

$$\log(\text{Biomass}) = 0.5690 * \log(\text{Volume}) - 1.51$$

$$p < 0.0001, r^2 = 0.7438$$

2004 Sagebrush Biomass

$$\log(\text{Biomass}) = 0.8629 * \log(\text{Volume}) - 4.7666$$

$$p < 0.0001, r^2 = 0.9062$$

Developed equations were then used to estimate sagebrush production on treatment plots. A plot mean was developed for canopy volume by measuring crown width and plant height of 50 sagebrush plants per treatment replicate. This value was used in the preceding equations to determine average production per sagebrush plant. This mean was then multiplied by the sagebrush density to estimate sagebrush production at the plot level. Density was determined by counting all rooted individuals in five 2 X 50 m belt transects.

Rabbitbrush production was determined by harvesting one 2 X 50 m belt transect per treatment replication. Harvested rabbitbrush was dried and current year's growth was removed and weighed to determine annual production.

Herbaceous cover and perennial herbaceous species density were visually estimated using 120 randomly located 0.2 m^2 frames per treatment replication. Shrub

cover was measured by line intercept (Canfield 1941) along five 50 m transect lines.

Total vegetation cover was the summation of the herbaceous and shrub cover.

Perennial herbaceous diversity was calculated from density values, using Hill's N1 and N2 equations (Hill 1973).

Photosynthetic rates were measured in the field every two weeks during the growing season, using a Li-Cor 6200 Portable Photosynthesis Unit on six randomly selected Thurber's needlegrass individuals per plot. Photosynthetic rates were converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$ by measuring leaf area with a Li-Cor 2100 Leaf Area Meter. Photosynthetic rates were used as an indicator of resource availability to herbaceous plant species, because decreases in soil water content and nitrogen availability have been reported to reduce photosynthetic rates in higher plants (Peek and Forseth 2003, Gyuga et al. 2002, Lawlor and Cornic 2002, Wingler et al. 1999).

Soil and Microtopography Sampling

Ten soil cores from both the 0-15 cm and 15-30 cm depths were collected from each treatment replication at two-week intervals during the growing season to measure soil water content. Water content of the soil cores was determined gravimetrically by drying at 100°C.

Total soil N, C, and OM in the upper 15 cm of the soil profile were determined from ten samples collected in July of each year from each treatment replication. Total

C and N were determined using a LECO CN 2000. Organic matter was estimated using an amended Rather method described in Nelson and Sommers (1982). Soil nitrate (NO_3^-) and ammonium (NH_4^+) content were measured by collecting four samples from each treatment in each block every month during the growing season. Each sample consisted of five compiled, 0-15 cm soil cores. Nitrogen fractions were extracted using 2N KCl solution. The extracted solution was analyzed for NO_3^- and NH_4^+ content by Oregon State University's Central Analytical Lab.

Microtopography was measured prior to burning and for two years post-burn, using four permanent 20 m transects per treatment replication. Microtopography was measured at 10 cm intervals along each transect. Measurements were determined using a transit and survey pole. Slope was calculated from the 200 measurements along each transect. Microtopography was reported as the standard deviation away from the transect slope. The change in microtopography was compared between treatments each year.

Statistical Analysis

Analysis of variance (ANOVA) models for a randomized block were used to test for differences in biomass production, soil water, soil inorganic nitrogen, soil total nitrogen and carbon, soil OM, Thurber's needlegrass photosynthetic rate, microtopography, herbaceous cover, and perennial vegetation diversity between

treatments (Table 6.1). Fisher LSD was used to test for differences between means. Differences between means were considered significant if p-values were less than 0.05.

Table 6.1. ANOVA models used to test for differences ($p < 0.05$) in treatments.

Variables	Degrees of Freedom
Biomass Production	
Block	5
Treatment	1
Residuals	5
Soil Water Content	
Block	5
Sampling Date	7
Treatment	1
Treatment:Date	7
Residuals	171
Soil Inorganic Nitrogen	
Block	5
Month	3
Treatment	1
Treatment:Month	3
Residuals	83
Total Soil C, N, and OM	
Block	5
Treatment	1
Residuals	5
Photosynthetic Rate	
Block	5
Sampling Date	4
Treatment	1
Treatment:Date	4
Residuals	105
Microtopography	
Block	5
Treatment	3
Residuals	15
Herbaceous Vegetation Cover, Diversity, and Biomass	
Block	5
Treatment	1
Residuals	5

Results

Soils

Soil Nitrogen, Carbon, and Organic Matter

NO_3^- and NH_4^+ content in the upper 15 cm of the soil profile were greater in the burned than control treatment in both years of the study ($p < 0.05$) (Fig. 6.1). NO_3^- averaged 0.26 mg/cm^3 (S.E. = 0.048) and 0.13 mg/cm^3 (S.E. = 0.027) greater in the burned than control treatment in 2003 and 2004, respectively. In 2003 and 2004, NH_4^+ was 0.52 mg/cm^3 (S.E. = 0.14) and 0.28 mg/cm^3 (S.E. = 0.09) greater in burned verses control treatment. Soil OM, total soil C, and total soil N were not different between treatments in either year of the study ($p > 0.05$) (Table 6.2).

Table 6.2. Soil OM, total C, and total N by treatment and year with standard error.

Soil Characteristic	Treatment	2003	2004
OM (%)	Burned	1.3±0.1	1.3±0.1
	Control	1.4±0.2	1.3±0.1
Total C (%)	Burned	0.9±0.1	0.8±0.1
	Control	0.9±0.1	0.8±0.1
Total N (%)	Burned	0.08±0.01	0.07±0.05
	Control	0.09±0.01	0.07±0.01

Different lower case letter indicates significant difference between treatments in that year ($p < 0.05$).

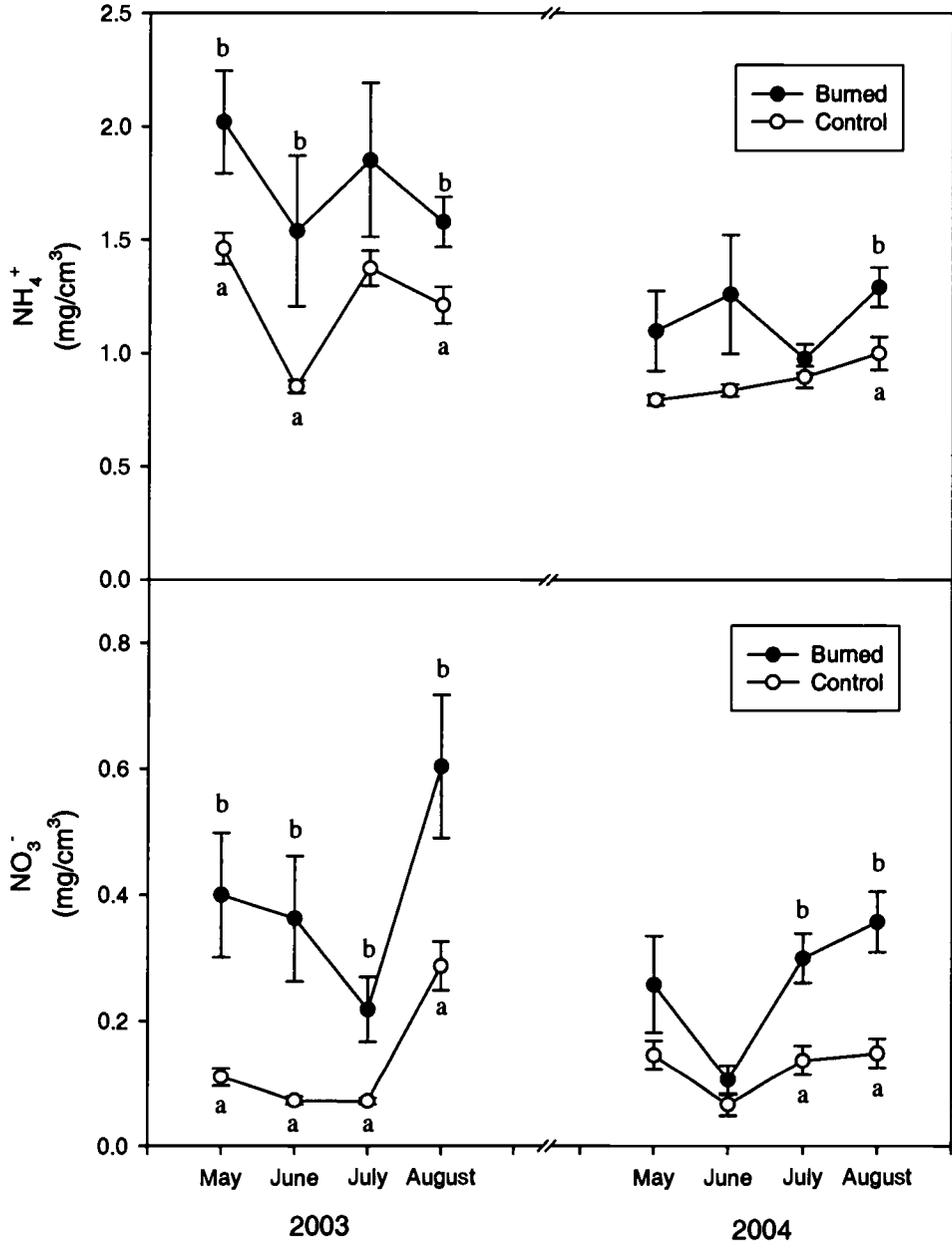


Figure. 6.1. NO_3^- and NH_4^+ content (mean \pm 1 standard error) in the upper 15 cm of the soil profile in burned and control treatments in 2003 and 2004. Different lower case letters indicate significant differences between treatments on that date ($p < 0.05$).

Soil Water

Soil water content in the 0-15 cm depth was different by treatment and date ($p < 0.05$), and the date by treatment interaction was significant in both 2003 and 2004 ($p < 0.05$). Soil water content in the 15-30 cm depth varied by treatment and date in both years of the study ($p < 0.05$), but the interaction between date and treatment was only significant in 2003. In both years, the control treatment had greater soil water content than the burned treatment during the growing season ($p < 0.05$) (Fig. 6.2). Across the growing season in 2003 and 2004, soil water content at the 0-15 cm depth was greater in the control than the burned treatment (2003: $p = 0.0019$, S.E. = 0.1579; mean = 7.9 and 7.5%, respectively, 2004: $p = 0.0062$, S.E. = 0.1548; mean = 7.9 and 7.4%, respectively). At the 15 to 30 cm depth, soil water content in the control treatment was greater than the burned treatment across the growing season in 2003 and 2004 (2003: $p = 0.0003$, S.E. = 0.1631; mean = 8.5 and 7.9 %, respectively, 2004: $p = 0.0426$, S.E. = 0.1513; mean = 8.2 and 7.9%). Soil water content appears to be mainly greater in control than the burned treatment early in the growing season and by June soil water content was relatively similar between treatments.

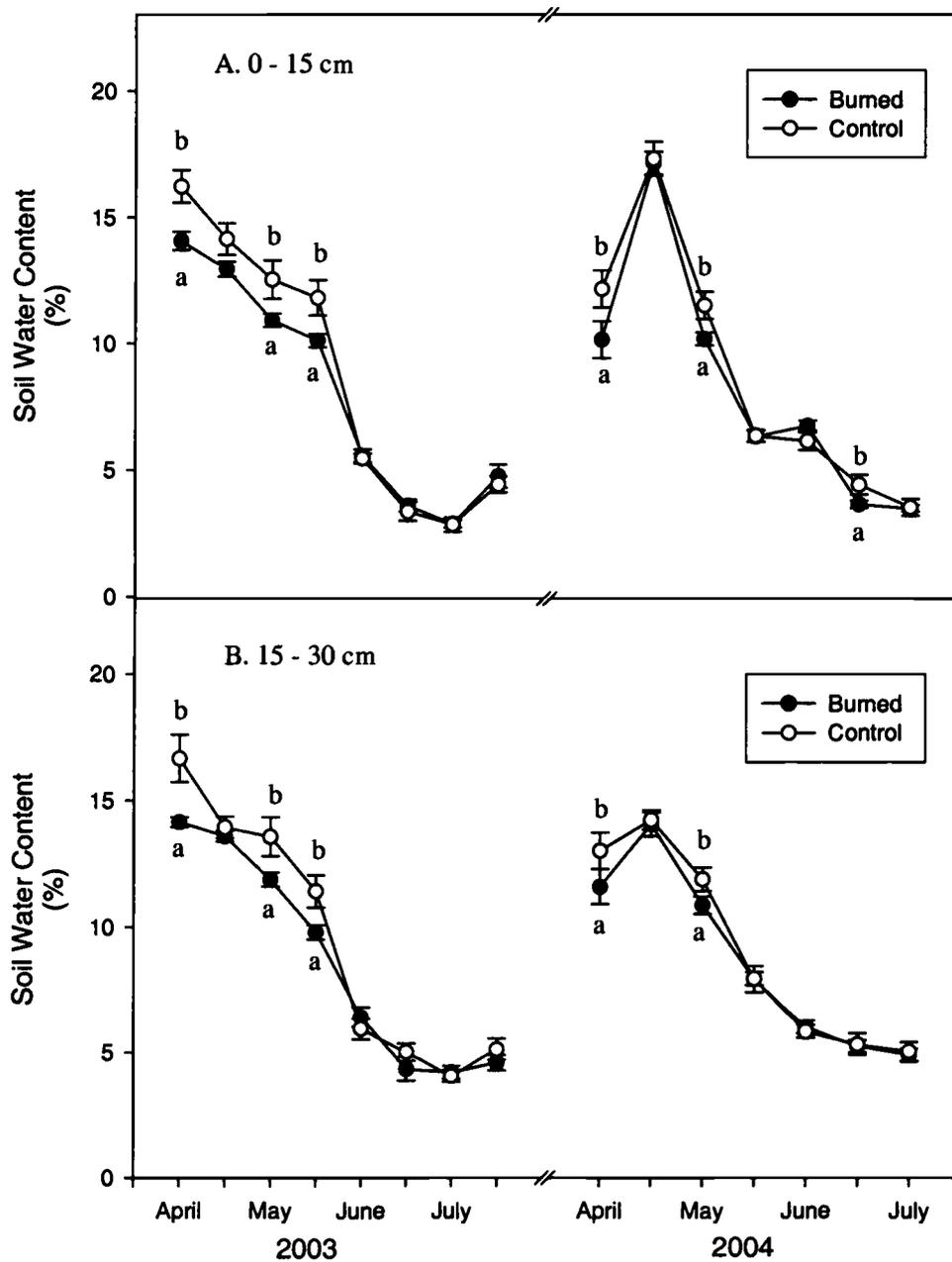


Figure 6.2. Soil water content (mean \pm 1 standard error) in; A. 0 – 15 cm and B. 15 – 30 cm depths. Different lower case letters indicate significant differences in soil water content between treatments on that sampling date ($p < 0.05$).

Microtopography

Change in microtopography was different between treatments the first year post-treatment ($p = 0.0101$). Microtopography decreased by 0.03 standard deviation of the transect slope (S.E. = 0.0104) more in the burned treatment in the first post-fire year than the control treatment. The change in microtopography in the burned treatment during the second post-fire year was not different from the control treatment ($p > 0.05$). Thus, microtopography decreased initially with sagebrush removal, but did not continue to decrease after the first post-burn year.

Vegetation

Biomass Production

Above-ground biomass production (shrub and herbaceous) was greater in the control than the burned treatment in 2003 and 2004 ($p = 0.0005$ and 0.0467 , respectively) (Table 6.3). However, the difference in biomass production between treatments became less in the second post-fire year. Herbaceous vegetation production in the burn was greater than in the control treatment in both years of the study ($p = 0.0264$ and 0.0037 , respectively). Tall tussock perennial bunchgrass production was greater in the burned than control treatments in 2003 and 2004 ($p = 0.0096$ and 0.0153 , respectively).

Table 6.3. Biomass production by treatment and year with standard error.

Vegetation	Treatment	Pre-treatment 2002 (kg/ha)*	2003 (kg/ha)	2004 (kg/ha)
Total Biomass	Burned	n.a.	339±19 a	676±63 a
	Control	n.a.	789±65 b	843±66 b
Total Herbaceous	Burned	423±33	321±16 b	657±62 b
	Control	487±52	254±14 a	338±20 a
Tall Tussock Perennial Grass	Burned	267±17	146±15 b	314±33 b
	Control	290±27	107±13 a	148±17 a
Sandberg bluegrass	Burned	n.a.	35±3.6 a	68±18
	Control	n.a.	76±8.2 b	73±12
Perennial Forb	Burned	n.a.	29±3.9	80±19
	Control	n.a.	21±4.0	53±9.0
Annual Grass	Burned	n.a.	0.89±0.28 b	0.11±0.1
	Control	n.a.	0.03±0.3 a	1.33±1.1
Annual Forb	Burned	n.a.	110±19 b	194±68
	Control	n.a.	40±11 a	62±22
Sagebrush	Burned	n.a.	0±0 a	0±0 a
	Control	n.a.	526±60 b	487±62 b
Rabbitbrush	Burned	n.a.	18±3.8	19±3.2
	Control	n.a.	17±3.3	18±3.5

Different lower case letter indicates significant difference between treatments in that year ($p < 0.05$).

* Standing crop = current and previous years' biomass still standing

Cover and Diversity

In the first post-fire year, herbaceous and total vegetation cover values were greater in the control than burned treatments (Table 6.4). By the second post-fire year, herbaceous cover was greater in the burned than control treatments. However, total

vegetation cover remained greater in the control than the burned treatment in the second post-fire year. Hill's N1 and N2 diversity indices (Hill 1973) for the perennial vegetation were not different between the control and burned treatment in either year of the study ($p > 0.05$) (Table 6.5).

Table 6.4. Vegetation cover by treatment and year with standard error.

Vegetation Cover	Treatment	2003	2004
Total Vegetation	Burned	17±0.8 a	26±2.1 a
	Control	40±2.4 b	36±3.1 b
Total Herbaceous	Burned	14±0.7 a	22±2.1 b
	Control	18±1.1 b	15±0.6 a
Tall Tussock Perennial Grass	Burned	5.0±0.4 a	7.2±0.8
	Control	7.5±0.8 b	6.0±0.8
Sandberg bluegrass	Burned	6.1±0.3	4.1±0.4
	Control	7.8±0.8	5.9±0.6
Perennial Forb	Burned	2.4±0.2	3.0±0.4
	Control	2.3±0.3	2.1±0.1
Annual Grass	Burned	0.01±0.01	0.04±0.02
	Control	0.01±0.01	0.01±0.00
Annual Forb	Burned	1.8±0.3	7.6±3.0
	Control	1.6±0.6	1.1±0.3
Sagebrush	Burned	0.0±0.0 a	0.0±0.0 a
	Control	10±1.03 b	13±1.6 b
Rabbitbrush	Burned	2.1±0.3 a	3.0±0.7
	Control	5.9±0.7 b	5.5±1.2

Different lower case letter indicates significant difference between treatments in that year ($p < 0.05$).

Table 6.5. Vegetation diversity by treatment and year with standard error.

Diversity Index	Treatment	2003	2004
Hill's N1	Burned	5.4 ±0.2	4.2 ±0.4
	Control	5.0 ±0.6	3.3 ±0.2
Hill's N2	Burned	3.0 ±0.1	6.2 ±0.5
	Control	3.5 ±0.3	5.6 ±0.4

Different lower case letter indicates significant difference between treatments in that year ($p < 0.05$).

Photosynthetic Rate

Photosynthetic rates of Thurber's needlegrass were different between treatments across the growing season and for several of the dates sampled in both years of the study ($p < 0.05$) (Figure 6.3). Photosynthetic rates varied by sampling date in 2003 and 2004, generally decreasing over the growing season ($p < 0.05$). In 2003, photosynthetic rates for Thurber's needlegrass averaged $1.48 \mu\text{mol m}^{-2} \text{s}^{-1}$ (S.E. = 0.4813) greater in the burned than control treatments during the growing season ($p = 0.0026$). In 2004, photosynthetic rates during the growing season averaged $1.86 \mu\text{mol m}^{-2} \text{s}^{-1}$ (S.E. 0.7485) greater in the burned than control treatments ($p = 0.0144$).

Discussion

We accepted our hypothesis that removing sagebrush with burning decreases resource capture and use in the two post-fire years. Greater biomass production and

vegetation cover in the control than burned treatment indicated that more solar energy was captured and resources were used when sagebrush was present in the community.

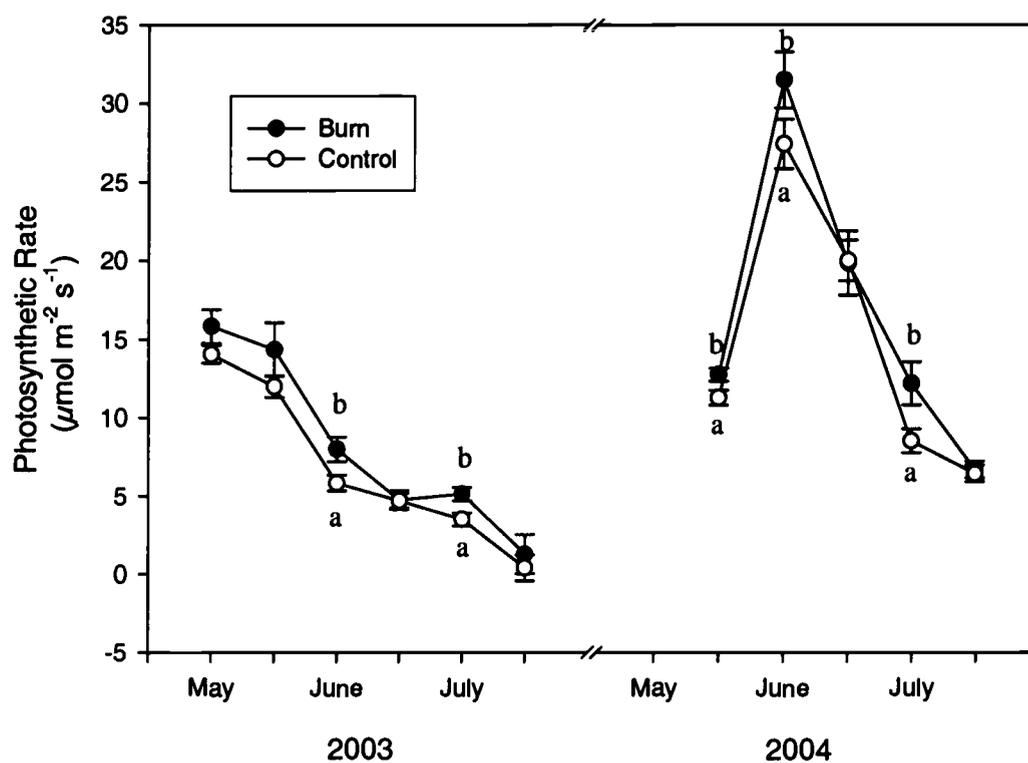


Figure 6.3. Photosynthetic rates (mean ± 1 standard error) of the burned and control treatments across the growing season in 2003 and 2004. Different lower case letters indicates a difference between treatments on that sampling date.

Harniss and Murray (1973) found similar production results when mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle) was removed with fire. They reported that thirty years after mountain big sagebrush was removed the unburned controls continued to produce more biomass annually than burned treatments.

However, herbaceous vegetation production was greater in the burned than control treatment by the first year after sagebrush removal and more than twofold greater by the second year. Other authors have reported similar and contrasting herbaceous production responses to sagebrush removal. Similar to our results, Hedrick et al. (1966), Sneva (1972), Harniss and Murray (1973), and Uresk et al. (1976) reported two to threefold increases in herbaceous production after sagebrush removal. In contrast to our results, Blaisdell (1953) and Peek et al. (1979) reported no significant changes in herbaceous production following burning sagebrush communities. Conflicting reports of herbaceous response to burning of sagebrush communities can be attributed to differing burn severity, post-fire weather, herbaceous species composition, and site characteristics. For example, Bates et al. (2004) reported that Wyoming big sagebrush/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) communities were less severely impacted and recovered more rapidly from wildfire than Wyoming big sagebrush/Thurber's needlegrass communities.

Herbaceous cover was greater in the burned than control treatment by the second post-treatment year. West and Hassen (1985) reported a similar herbaceous cover response in a Wyoming big sagebrush community in Utah. However, much of their increase in herbaceous cover was cheatgrass. The lag in herbaceous cover in our burned treatment was the result of a delayed response in herbaceous plants to increased resource availability. Bates et al. (2000) reported a similar lag in herbaceous response to western juniper (*Juniperus occidentalis* Hook.) removal.

Microtopography, important in reducing runoff, erosion, and nutrient loss, and in increasing infiltration (Dunne et al. 1991, Eltz and Norton 1997), initially decreased with sagebrush removal. Microtopography ceased to significantly change after one year, but the study site was in high seral condition and the perennial bunchgrass component exceeded pre-burn cover levels by the second year following sagebrush removal. Microtopography would have decreased further due to erosion if the study area was on steeper terrain or if there was greater perennial herbaceous mortality. The potential for erosion increases with steepness of slope and greater vegetation mortality (McNabb and Swanson 1990).

Lower growing season soil water content in the burned compared to the control treatment suggests the loss of sagebrush reduced water capture. Obrist et al. (2004) also reported greater soil water content in a control than burned treatment in a big sagebrush community at the start of the growing season. Contrary to our results, removal of western juniper (Bates et al. 2000), pinyon-juniper (*Pinus edulis* Engelm – *Juniperus osterosperma* (Torr.) Little) (Gifford and Shaw 1973), and Gambel oak (*Quercus gambelii* Nutt.) (Marquiss 1972) resulted in increased soil water content. These contradictions with our results could be due to site characteristics, water acquisition patterns, and/or interactions with other plant species. Wyoming big sagebrush is a much smaller plant and generally occupies more arid sites than western juniper, pinyon-juniper, and Gambel oak, which could account for the contradiction. Lower soil water content in the burned treatment was either due to decreased initial

capture, increased evaporation, or a combination of both factors. The removal of sagebrush in the burned treatment may have reduced snow capture. Hutchison (1965) reported that sagebrush communities had higher accumulations of snow than adjacent grasslands. Sturges (1977) reported snow accumulations were reduced where mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* (Rydb.) Beetle) was removed, compared to where it remained until snow completely covered the sagebrush.

Even with less soil water content early in the season, Thurber's needlegrass photosynthetic rates were greater in the burned than control plots. Higher photosynthetic rates suggest that resource availability to herbaceous vegetation was greater in the burned than control treatment. Higher concentrations of NO_3^- and NH_4^+ may have contributed to higher photosynthetic rates in the burned treatment. Increased nitrogen availability (Peek and Forseth 2003, Gyuga et al. 2002) and/or water availability (Lawlor and Cornic 2002, Wingler et al. 1999) can result in higher photosynthetic rates. The removal of a competitor can increase the availability of soil water (Bates et al. 2000). Williams et al. (1991) reported that bluebunch wheatgrass and desert wheatgrass carbon isotope ratios indicated more water was available to them when they didn't experience competition with big sagebrush. Removing Wyoming big sagebrush increased the availability of resources, resulting in higher Thurber's needlegrass photosynthetic rates in the burned treatment. The twofold increase in the herbaceous biomass production with sagebrush removal also indicates

resources were more available to herbaceous vegetation in the burned than control treatment.

The increase in herbaceous production and simultaneously Thurber's needlegrass photosynthetic rates in the burned compared to the control treatment indicates resources were not fully utilized or captured in the burned treatment two years post-burning. When resources are not fully exploited, an opportunity may exist for other plant species to become established or increase.

Excess resources in the burned treatment provide opportunities to establish/increase desired vegetation. Wirth and Pyke (2003) reported that seeding success of three perennial forbs was greater in a burned than unburned Wyoming big sagebrush community. Our results indicate livestock forage can be increased by prescribed fall burning relatively intact, late seral Wyoming big sagebrush communities. However, the risk of weed invasion greatly increases with increased soil resource availability (Sheley et al. 1999b, Svejcar 2003). Sheley et al. (1999a) suggested that plant communities of the Intermountain Region must use soil resources, especially soil moisture, to remain weed-resistant.

Herbaceous perennial vegetation diversity was not different between the burned and control treatments. This was attributed to limited plant mortality in the prescribed burn. Humphrey (1984) reported a similar lack of differences in diversity between unburned and burned big sagebrush communities in southeastern Idaho and suggested that it was a result of most of the perennial vegetation surviving the burn. Our study

sites were opened up with burning and we measured primarily a perennial response to the excess resources. However, there was an increase in *Alyssum* L. sp., an introduced annual plant. *Alyssum* sp. do not appear to significantly hinder site recovery (Bates et al. 2005). The rapid response of perennials or the limited readily available noxious weed propagules source for colonization may have prevented noxious weed encroachment. Had there been a source of noxious weed propagules near the study site and/or increased herbaceous mortality, noxious weeds may have invaded the burned treatment.

Management Implications

Our study is limited to the impacts of removing sagebrush with prescribed fall burning on relatively intact, late seral Wyoming big sagebrush communities without a readily available source of noxious weed propagules and limited mortality of perennial herbaceous vegetation. However, the results indicated some of the potential impacts of the loss of big sagebrush from plant communities and the need for long-term studies of resource capture after Wyoming big sagebrush removal with burning. Community resource capture and utilization decreased when Wyoming big sagebrush was removed with fire and had not returned to pre-burn levels after two years. How long community resource capture and use remains below pre-burn levels needs to be investigated and is probably influenced by site factors, burn severity, and post-burning

climatic conditions. The presence of sagebrush and an intact herbaceous understory, which fully utilizes available resources, is important to maintaining weed resistance. Removing Wyoming big sagebrush to increase herbaceous production or alter wildlife habitat should be undertaken with caution because of the threat of introduced annual grasses.

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CHAPTER 7

GENERAL CONCLUSION

Relatively intact, late seral Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* (Beetle & A. Young) S.L. Welsh)¹ communities vary greatly in their biological potential. The variability in vegetation characteristics was not strongly correlated with environmental characteristics, making management difficult. A limited understanding of the variability across the sagebrush biome has resulted in application of vegetation requirements that are beyond the biological potential of many sagebrush communities. The role of Wyoming big sagebrush within the plant community has generally been ignored.

We sampled 107 intact, late seral Wyoming big sagebrush sites in eastern Oregon and a small portion of northern Nevada. Five associations based on dominant tall tussock perennial bunchgrass were designated: bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & J.G. Sm.), Thurber's needlegrass (*Stipa thurberiana* Piper), needle-and-thread (*Stipa comata* Trin. & Rupr.), Idaho fescue (*Festuca idahoensis* Elmer), and bluebunch wheatgrass-Thurber's needlegrass associations. Vegetation cover and composition varied substantially among these associations, thus

¹ Nomenclature follows Hitchcock, C.L., and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press. Seattle, WA. 730 p.

indicating that separating the Wyoming big sagebrush alliance into associations is useful for land management purposes.

The variability in vegetation cover and composition of this alliance cautions against applying specific vegetation requirements to manage sagebrush rangelands. Community cover and height attributes measure in our study indicate that sage-grouse habitat vegetation requirements developed by the Bureau of Land Management et al. (2000) and Connelly et al. (2000) should not be used to manage the Wyoming big sagebrush alliance in eastern Oregon. The failure of these guidelines in the Wyoming big sagebrush alliance was the result of requirements being beyond the basic vegetation potentials of this alliance. The requirements were erroneously high because they were developed from small-scale studies that do not apply to the stand, community, or landscape level. We question using guidelines developed for one species to manage sagebrush communities, as they ignore the fact that there are multiple sagebrush facultative and obligate species with differing habitat requirements. The Wyoming big sagebrush alliance needs to be managed with the needs of multiple species in mind and an understanding of the inherent variability in the system.

Though vegetation cover and structure were highly variable, little of this variability could be explained by environmental characteristics. Total herbaceous cover was the vegetation characteristic best explained by environmental characteristics. About half of the total herbaceous cover variation was explained by

soil water holding capacity, incidental radiation, depth to Bt soil horizon, and percentage of sand in the upper 15 cm of the soil profile. Variation in species composition among sites was mainly correlated to soil differences. The most common species abundances appear dependent upon soil characteristics in the upper 15 cm of the profile, but correlations were generally not strong enough to be useful predictors.

With a few exceptions, the environmental relationships to vegetation characteristics in the Wyoming big sagebrush alliance were obscure and had limited usefulness for management. One exception was that environmental factors could be used to roughly estimate a site's ability to produce herbaceous cover. The wide ecological amplitude of plant species generally prevents more specific predictions of vegetation characteristics from environmental factors within the Wyoming big sagebrush alliance.

To investigate the influence of sagebrush on microsites (subcanopy and interspace), herbaceous vegetation, and community resource capture and use, we randomly selected twelve plots at the Northern Great Basin Experimental Range (NGBER) and another four plots at Baker Pass. Half of the plots were burned at the NGBER to determine the influence of sagebrush on community resource capture and use with fire as the driving disturbance mechanism. Within individual stands, Wyoming big sagebrush impacted microsite characteristics, vegetation biomass, cover, and density heterogeneity, and community resource capture. The subcanopy appears to be a more favorable microsite for herbaceous vegetation, compared to the interspace

at sites with high incidental radiation. However, vegetation characteristics did not exhibit clear zonal differences at sites with lower incidental radiation. This indicates that the influence Wyoming big sagebrush has on associated herbaceous vegetation is site and species dependent.

Removing Wyoming big sagebrush with prescribed fire impacted community resource capture and utilization. Burning these sagebrush rangelands increased herbage production. Burning sagebrush rangelands also opens the community up to plant colonization as resources are not fully utilized the first two years post-fire. The potential for weed invasion would greatly increase if the herbaceous component was severely damaged by fire. Sagebrush is also important to many wildlife species; thus, any removal plans should consider the consequences to wildlife. The impacts Wyoming big sagebrush has on community resources capture and utilization strongly argues that caution should be employed when considering sagebrush control.

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APPENDICES

Appendix 1. Habitat requirements from sage-grouse management guidelines.

Bureau of Land Management et al. (2000) habitat requirements for greater sage-grouse.

	Optimum Nesting		Optimum brood-rearing		Suboptimum brood-rearing		Wintering	
	Height (cm)	Canopy (%)	Height (cm)	Canopy (%)	Height (cm)	Canopy (%)	Height (cm)	Canopy (%)
Sagebrush	40 – 80	15 – 25	40 – 80	10 – 25	40 – 80	≥ 14	≥ 25 - 30 ^b	10 – 30
Grass-forb	≥ 18	25 ^a	≥ 18	25 ^a	≥ 18	15	N/A	N/A
Area ^c	> 80		> 40		> 40		> 80	

^a at least 15% grass canopy cover and 10% forb canopy cover

^b at least 25 to 30 cm exposed above the snow level

^c percentage of seasonal habitat needed with indicated conditions

Connelly et al. (2000) habitat requirements for greater sage-grouse.

Mesic Breeding = 15 - 25% sagebrush cover between 40 and 80 cm tall, at least 15% grass canopy cover and 10% forb canopy cover over 18 cm tall.

Mesic Brood Rearing = 10 - 25% sagebrush cover between 40 and 80 cm tall, at least 15% combined grass-forb canopy cover.

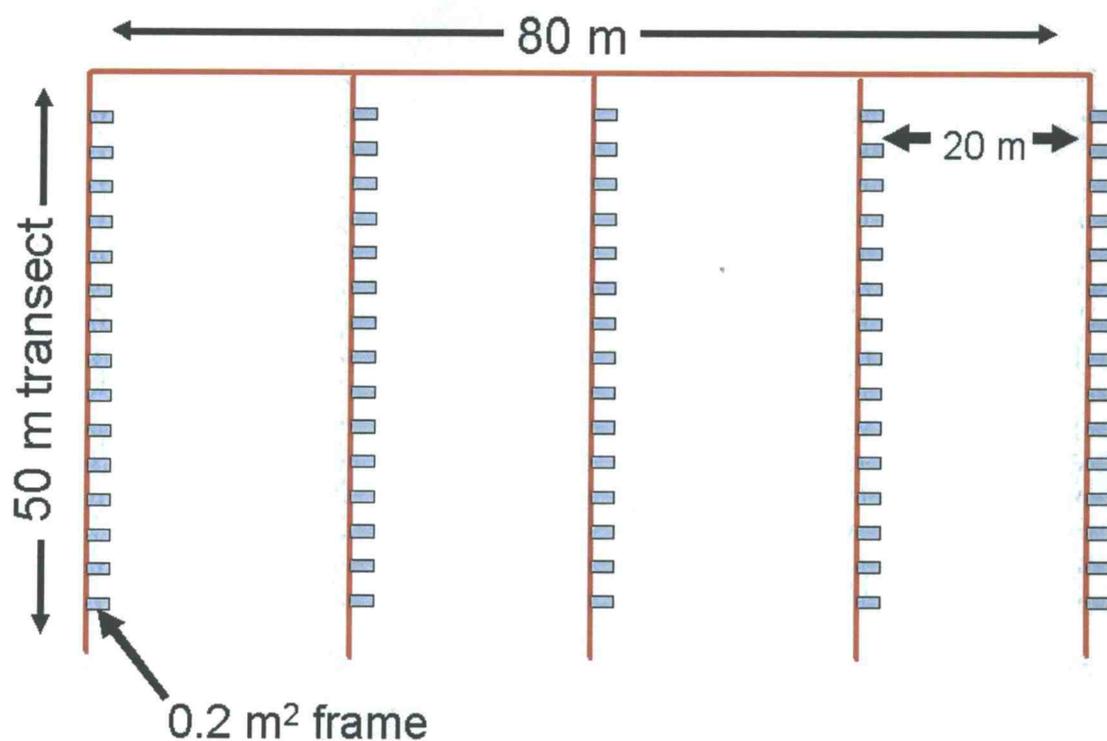
Mesic Winter = 10 - 30% sagebrush cover 25 to 30 cm exposed above the snow.

Arid Breeding = 15 - 25% sagebrush cover between 40 and 80 cm tall, at least 15% combined grass-forb canopy cover.

Arid Brood Rearing = 10 - 25% sagebrush cover between 40 and 80 cm tall, at least 15% combined grass-forb canopy cover

Arid Winter = 10 - 30% sagebrush cover 25 to 30 cm exposed above the snow.

Appendix 2. Plot layout for sampling vegetation cover.



- Shrub cover = line intercept along 50 m transects
- Herbaceous cover = visual estimated by species using 0.2 m² frames (15 per transect)

Appendix 3 continued. Species list for Wyoming big sagebrush sites sampled in the study area.

Scientific name	Common name	Scientific name	Common name
<u>Perennial Forbs cont.</u>		<u>Perennial Forbs cont.</u>	
<i>Crepis intermedia</i>	tapertip or grey hawksbeard	<i>Lupinus arbustus</i>	perfume lupine
<i>Crepis modocensis</i>	modoc hawksbeard	<i>Lupinus argenteus</i>	silvery lupine
<i>Crepis occidentalis</i>	western hawksbeard	<i>Lupinus caudatus</i>	tailcup lupine
<i>Cryptantha humilis</i>	roundspike cryptantha	<i>Lupinus leucophyllus</i>	velvet lupine
<i>Delphinium andersonii</i>	desert or Anderson's larkspur	<i>Lygodesmia spinosa</i>	spiny skeletonweed
<i>Delphinium bicolor</i>	little Montane larkspur	<i>Machaeranthera canescens</i>	hoary aster
<i>Delphinium depauperatum</i>	slim or dwarf larkspur	<i>Malacothrix glabrata</i>	smooth desertdandelion
<i>Delphinium nuttallianum</i>	upland larkspur	<i>Malacothrix torreyi</i>	Torrey's desertdandelion
<i>Dodecatheon pauciflorum</i>	darkthroat shooting star	<i>Mentzelia laevicaulis</i>	lemon flwr'd blazing star
<i>Erigeron aphanactis</i>	rayless shaggy fleabane	<i>Mertensia longiflora</i>	long-flowered bluebells
<i>Erigeron bloomeri</i>	scabland fleabane	<i>Mertensia oblongifolia</i>	sagebrush bluebells
<i>Erigeron chrysopsidis</i>	dwarf yellow fleabane	<i>Microseris nutans</i>	nodding microseris
<i>Erigeron filifolius</i>	thread-leaf fleabane	<i>Microseris troximoides</i>	false agoseris
<i>Erigeron linearis</i>	desert yellow daisy	<i>Oenothera caespitosa</i>	tufted evening-primrose
<i>Erigeron poliospermus</i>	cushion fleabane	<i>Oenothera deltoides</i>	hairy eve.-primrose
<i>Erigeron pumilus</i>	shaggy fleabane	<i>Oenothera tanacetifolia</i>	tansy-leaf evening
<i>Eriogonum caespitosum</i>	mat buckwheat	<i>Penstemon cusikii</i>	Cusick's penstemon
<i>Eriogonum douglasii</i>	Douglas' buckwheat	<i>Penstemon deustus</i>	scabland penstemon
<i>Eriogonum microthecum</i>	slenderbush eriogonum	<i>Penstemon humilis</i>	lowly penstemon
<i>Eriogonum ochrocephalum</i>	whitewoolly buckwheat	<i>Penstemon laetus</i>	gay penstemon
<i>Eriogonum ovalifolium</i>	cushion buckwheat	<i>Penstemon speciosus</i>	showy penstemon
<i>Eriogonum sphaerocephalum</i>	round-headed eriogonum	<i>Perideridia bolanderi</i>	Bolander's yampah
<i>Eriogonum strictum</i>	strict buckwheat	<i>Phacelia hastata</i>	silverleaf phacelia
<i>Eriogonum umbellatum</i>	sulfur buckwheat	<i>Phlox hoodii</i>	Hood's phlox
<i>Eriophyllum lanatum</i>	Oregon sunshine	<i>Phlox longifolia</i>	long-leaf phlox
<i>Frasera albicaulis</i>	white-stemmed frasera	<i>Phlox muscoides</i>	moss or musk phlox
<i>Fritillaria pudica</i>	yellow bell	<i>Phoenicautis cheiranthoides</i>	daggerpod
<i>Halogeton glomeratus</i>	saltlover, halogeton	<i>Ranunculus glaberrimus</i>	sagebrush buttercup
<i>Haplopappus acaulis</i>	stemless goldenweed	<i>Scutellaria angustifolia</i>	narrowleaf skullcap
<i>Haplopappus stenophyllus</i>	narrow-leaf goldenweed	<i>Scutellaria antirrhinoides</i>	snappedragon or nose
<i>Leptodactylon pungens</i>	prickly phlox	<i>Scutellaria nana</i>	dwarf scutellaria
<i>Lewisia rediviva</i>	bitterroot	<i>Senecio canus</i>	woolly groundsel
<i>Linum perenne</i>	blue flax	<i>Senecio integerrimus</i>	one-stemmed butterweed
<i>Lithospermum ruderale</i>	stoneseed	<i>Silene douglasii</i>	Douglas' silene
<i>Lomatium sp.</i>	biscuit-root	<i>Townsendia florifera</i>	showy Townsend daisy
<i>Lomatium cous</i>	Cous	<i>Townsendia hookeri</i>	Hooker's Townsend daisy
<i>Lomatium donnellii</i>	Donnell's desert-parsley	<i>Trifolium andersonii</i>	fiveleaf clover
<i>Lomatium dissectum</i>	giant lomatium	<i>Trifolium macrocephalum</i>	big-head clover
<i>Lomatium foeniculaceum</i>	desert parsley or biscuitroot	<i>Verbascum thapsus</i>	common mullein
<i>Lomatium macrocarpum</i>	large-fruit lomatium	<i>Viola beckwithii</i>	Beckwith's violet
<i>Lomatium nevadense</i>	Nevada desert-parsley	<i>Viola purpurea</i>	purplish violet
<i>Lomatium packardiae</i>	Malheur lomatium	<i>Viola trinervata</i>	desert pansy, Rainier
<i>Lomatium triternatum</i>	nine-leaf lomatium	<i>Zigadenus paniculatus</i>	panicked death-camas
<i>Lomatium vaginatum</i>	broadsheath lomatium	<i>Zigadenus venosus</i>	meadow death-camas

Appendix 3 continued. Species list for Wyoming big sagebrush sites sampled in the study area.

Scientific name	Common name	Scientific name	Common name
<u>Annual Forbs</u>		<u>Annual Forbs cont.</u>	
<i>Agoseris heterophylla</i>	annual agoseris	<i>Layia glandulosa</i>	white daisy tidytips
<i>Alyssum alyssoides</i>	pale alyssum	<i>Linanthus pharamaceoides</i>	thread-stemmed linanthus
<i>Alyssum desertorum</i>	desert alyssum	<i>Linanthus septentrionalis</i>	northern linanthus
<i>Amsinckia tessellata</i>	tessellate fiddleneck	<i>Lupinus brevicaulis</i>	sand or short stmed lupine
<i>Blepharipappus scaber</i>	rough eyelashweed	<i>Lupinus microcarpus</i>	chick lupine
<i>Camissonia claviformis</i>	club-frt. eve.-primrose	<i>Lupinus uncialis</i>	lilliput or inch-high lupine
<i>Camissonia scapoidea</i>	Piaute suncup	<i>Madia</i> sp.	tarweed; madia
<i>Chaenactis macrantha</i>	bighead dustymaiden	<i>Madia exigua</i>	little tarweed
<i>Chaenactis xantiana</i>	flesh color pincushion	<i>Madia gracilis</i>	gumweed; common
<i>Cirsium</i> sp.	thistle	<i>Mentzelia albicaulis</i>	white-stemmed mentzelia
<i>Cirsium utahense</i>	Utah thistle	<i>Microsteris gracilis</i>	pink microsteris
<i>Cirsium vulgare</i>	spear, bull or common thistle	<i>Microsteris lindleyi</i>	Lindley's microsteris
<i>Clarkia pulchella</i>	pink fairies; ragged robbin	<i>Mimulus</i> sp.	monkey-flower
<i>Collinsia parviflora</i>	little blue-eyed Mary	<i>Mimulus cusickii</i>	Cuskick's monkey flower
<i>Collomia grandiflora</i>	large-flowered collomia	<i>Mimulus nanas</i>	dwarf purple monkey
<i>Collomia linearis</i>	narrow-leaf collomia	<i>Mimulus sudsdorfii</i>	Suksderf's monkey flower
<i>Cryptantha</i> sp.	white forget-me-not	<i>Navarretia breweri</i>	yellow-flowered navarretia
<i>Cryptantha ambigua</i>	obscure cryptantha	<i>Navarretia divaricata</i>	white-flowered mt.
<i>Cryptantha circumscissa</i>	cushion cryptantha	<i>Orthocarpus hispidus</i>	hairy owl-clover
<i>Cryptantha intermedia</i>	common cryptantha	<i>Phacelia humilis</i>	low phacelia
<i>Cryptantha torreyana</i>	Torrey's cryptantha	<i>Phacelia linearis</i>	thread-leaf phacelia
<i>Cryptantha watsonii</i>	Watson's cryptantha	<i>Plectritis macrocera</i>	white plectritis
<i>Descurainia pinnata</i>	western tansymustard	<i>Polemonium micranthum</i>	annual littlebells
<i>Draba verna</i>	spring whitlow	<i>Polygonum douglasii</i>	Douglas' knotweed
<i>Epilobium minutum</i>	sm.-flwed willowweed	<i>Ranunculus testiculatus</i>	hornseed or bur buttercup
<i>Epilobium paniculatum</i>	autumn willow-herb	<i>Sisymbrium altissimum</i>	Hill tumble mustard
<i>Eriastrum sparsiflorum</i>	few-flowered eriastrum	<i>Tragopon dubis</i>	yellow salsify
<i>Eriogonum cernuum</i>	nodding buckwheat		
<i>Eriogonum maculatum</i>	spotted buckwheat		
<i>Eriogonum vimineum</i>	broom buckwheat		
<i>Galium aparine</i>	goose-grass		
<i>Galium bifolium</i>	low mountain bedstraw		
<i>Gayophytum decipiens</i>	deceptive groundsmoke		
<i>Gayophytum diffusum</i>	spreading groundsmoke		
<i>Gayophytum racemosum</i>	blackfoot groundsmoke		
<i>Gayophytum ramosissimum</i>	pinyon groundsmoke		
<i>Gilia capillaris</i>	miniature gilia		
<i>Gilia inconspicua</i>	shy, or sinuate gilia		
<i>Gilia leptomeria</i>	sand gilia		
<i>Gilia sinuata</i>	sinuate gilia, rosy gilia		
<i>Lactuca serriola</i>	prickly lettuce		

Appendix 4. Vegetation and ground cover (%) summaries for each plot.

PLOT	Sandberg bluegrass	Perennial Grass	Annual Grass	Perennial Forb	Annual Forb	Litter	Baraground & Rock	Moss & Crust	Wyo. big sagebrush	Other Shrub	Tall Forb (≥18 cm)
ANTELO	4.76	9.56	0.60	1.52	0.26	17.70	60.43	5.47	15.89	1.26	0.91
BABOON	0.03	10.19	1.13	0.65	0.32	13.68	73.92	0.23	3.20	1.59	0.36
BLACK	4.29	11.69	0.07	6.45	1.02	17.81	52.74	6.15	17.84	0.28	3.63
BLOODA	4.24	12.51	0.00	1.49	0.56	8.06	62.10	11.21	7.96	0.00	0.48
BLOODB	5.69	6.56	0.02	1.45	0.60	15.49	57.18	13.18	10.92	0.00	0.51
BOWEN	8.44	7.79	0.00	2.30	0.41	18.84	60.47	2.29	13.04	1.50	1.36
BUCKA	5.49	11.84	0.00	7.72	0.35	13.90	55.71	5.43	11.04	0.68	2.73
BUCKB	6.87	7.84	0.00	11.69	0.33	7.72	50.08	15.71	8.10	0.00	6.83
BUZZB	4.27	9.69	0.06	6.24	0.32	14.92	56.99	7.59	14.81	1.82	3.93
CASSIDY	6.56	10.15	0.18	6.74	1.66	14.26	53.44	8.89	7.20	1.28	0.55
CLOVERA	7.49	13.51	0.43	3.33	0.57	16.76	53.75	4.77	15.45	0.96	1.36
COVERS	4.61	8.94	3.72	2.63	0.34	19.30	61.17	1.38	14.86	6.58	1.38
COFFINB	7.12	7.71	0.06	5.03	0.18	15.55	59.73	4.97	12.76	0.00	0.93
COFFINC	7.81	13.28	0.30	2.27	0.33	12.57	60.47	3.92	10.63	0.00	0.14
COFFIND	6.65	7.80	0.26	2.61	0.38	11.47	65.61	5.97	13.67	0.00	0.53
DEADA	9.40	8.79	0.00	11.58	0.37	15.65	40.08	14.30	12.18	0.00	7.15
DEADB	6.67	11.37	0.00	10.59	0.34	18.31	42.01	10.86	7.39	0.00	9.59
DEADC	3.52	9.09	1.21	2.25	0.09	27.26	55.30	1.39	13.75	0.42	0.66
DEADD	6.81	18.07	0.00	5.89	0.41	13.91	48.00	9.01	10.82	0.22	3.50
DEERA	4.66	22.88	9.82	3.20	1.18	24.65	30.86	4.09	4.58	2.11	2.50
DEERN	6.68	16.57	2.76	3.62	0.77	17.24	44.36	8.53	10.30	4.40	2.06
DEERNN	5.97	28.31	0.19	2.99	1.32	20.56	33.53	7.81	16.00	1.81	1.71
DEERW	4.89	16.07	7.64	4.07	1.24	16.84	48.81	3.28	6.18	6.52	1.29
DRYA	1.33	13.09	0.08	2.43	0.45	10.35	62.39	10.02	10.20	0.84	0.61
DRYB	4.24	6.96	0.00	0.33	0.57	13.25	65.60	9.15	11.54	1.02	0.25
EGLIA	5.28	9.05	0.06	4.22	5.60	15.87	55.32	4.68	9.63	0.00	2.22
EXCA	0.00	4.55	1.08	0.00	0.24	22.76	62.30	9.15	11.03	0.53	0.23
EXCB	0.00	5.39	0.30	0.15	0.48	12.72	74.77	6.27	5.16	4.48	0.34
FFC	8.98	10.67	0.00	10.57	0.23	13.20	48.59	10.54	10.16	1.20	1.30
FFD	9.92	18.32	0.00	6.41	0.37	16.60	41.76	8.16	7.56	0.00	5.16
FFE	7.24	10.76	0.05	2.86	0.18	14.14	63.48	2.10	12.24	0.00	0.80
FFF	7.00	10.34	0.03	10.44	0.37	12.22	53.03	7.71	11.40	0.00	1.55
FFG	6.26	9.48	3.48	3.09	0.22	16.71	61.35	0.52	8.76	0.00	0.42
FFM	13.21	11.41	0.02	11.90	0.62	8.24	44.34	12.03	15.11	0.00	9.36
FFS	7.81	7.95	0.15	2.93	0.70	13.45	62.03	5.73	19.15	0.00	0.27
FUNA	6.65	12.41	0.06	2.59	0.09	17.91	53.15	7.20	11.92	0.17	1.29
FUNB	5.49	9.59	0.02	2.05	0.42	14.13	60.15	8.24	9.61	2.55	1.15
GAPB	6.45	10.19	0.00	4.24	0.39	12.19	57.63	9.35	8.92	2.06	1.53
GLBA	3.47	20.64	0.00	2.03	0.02	11.89	57.31	4.84	13.71	0.88	0.23
GLBB	5.33	14.70	0.24	1.56	0.09	21.87	53.64	2.87	15.37	1.60	0.87
GLBC	6.27	8.76	0.00	3.24	0.08	14.08	64.00	3.84	11.37	0.57	1.86
GLBD	6.79	12.15	0.00	4.10	0.05	12.67	56.34	8.37	8.26	2.28	2.00
GLBE	5.07	20.80	0.00	1.23	0.09	15.42	55.09	2.62	7.96	1.42	0.05

Appendix 4 continued. Vegetation and ground cover (%) summaries for each plot.

PLOT	Sandberg bluegrass	Perennial Grass	Annual Grass	Perennial Forb	Annual Forb	Litter	Bareground & Rock	Moss & Crust	Wyo. big sagebrush	Other Shrub	Tall Forb (≥18 cm)
GRAVEL	2.66	26.73	0.00	5.47	0.05	13.67	36.89	14.57	9.54	0.40	1.21
HIHOS	3.30	17.90	0.00	4.63	0.52	11.67	58.57	3.15	6.03	2.63	3.09
HILLBILL	6.51	11.32	0.01	5.86	0.11	10.43	59.27	6.75	19.30	0.11	3.10
HTHA	6.61	8.34	0.14	5.08	0.35	13.78	57.70	8.25	15.66	1.42	2.56
HTHB	5.04	17.37	0.03	3.91	0.47	16.67	50.63	6.14	11.92	8.17	2.35
IPITY	7.18	15.13	0.02	5.74	0.24	14.58	51.69	5.57	9.74	0.36	1.27
INDECENT	7.28	9.21	0.00	4.37	0.28	12.14	58.86	7.98	11.89	0.09	0.60
JCKIPU	2.28	15.21	2.75	0.41	2.37	11.68	50.49	15.82	6.72	2.00	0.39
JON	4.90	8.47	1.37	2.45	1.32	17.26	62.64	1.76	9.01	0.00	0.63
LCLC	5.05	9.17	0.00	7.30	0.96	20.26	52.64	4.90	12.85	0.48	3.00
LILY	4.24	10.69	0.01	2.29	0.44	11.93	58.05	12.66	10.20	1.39	1.07
LIZARD	7.04	19.64	2.63	3.05	0.50	17.40	42.87	7.80	13.00	4.85	2.74
LONEBUT	3.93	16.16	1.71	0.31	0.03	21.35	53.01	3.23	10.78	0.00	0.08
LONEMT	3.98	10.61	0.91	1.18	0.26	18.13	60.69	4.43	10.02	0.33	0.53
LUCKY	6.76	11.17	0.01	3.89	0.49	14.97	54.59	8.52	13.55	0.69	2.80
MOOH	5.36	7.65	0.00	3.43	0.36	12.53	63.63	7.21	7.90	1.45	1.14
MOOHEX	5.61	13.82	0.00	6.11	0.25	17.35	52.81	4.29	14.70	1.28	3.29
MULEA	6.52	10.03	0.27	4.12	0.14	11.47	61.13	6.62	13.90	0.10	2.73
MULEB	6.20	16.31	0.00	3.95	0.25	13.69	55.14	4.58	15.88	0.40	2.18
MULEC	3.08	8.90	0.14	0.53	0.35	20.22	57.71	9.18	21.44	0.82	0.38
MULED	4.92	16.07	0.01	3.03	0.17	11.54	52.82	11.56	15.92	0.72	1.11
MULEE	1.82	9.61	3.11	0.93	0.06	14.79	68.65	1.14	17.40	0.26	0.26
OAR	4.65	21.75	0.03	7.54	0.61	7.24	55.91	4.00	12.94	0.00	0.49
PAINT	5.06	11.04	0.55	3.36	0.40	21.45	57.03	1.49	11.52	5.73	2.42
PATTONA	4.48	7.96	1.20	4.21	0.40	15.05	62.73	4.26	9.37	0.42	0.99
POACH	8.52	9.94	0.03	7.32	0.89	18.16	51.99	3.40	9.92	1.19	4.73
QUINN	4.16	8.66	0.11	4.90	0.31	16.74	60.97	4.37	20.79	0.15	1.54
RANGT	5.78	9.47	0.00	6.80	3.05	16.78	55.82	3.85	19.77	0.71	4.47
RANGTW	5.87	13.53	0.09	4.43	1.02	11.27	63.63	2.06	15.77	0.96	0.69
ROUNDA	4.11	11.83	1.18	0.84	0.32	13.51	65.17	3.21	12.48	0.00	0.63
RUNA	4.07	7.16	1.86	10.97	0.57	16.19	52.17	7.19	17.15	0.88	10.56
RUNB	6.57	8.20	2.00	2.99	1.03	17.92	58.96	2.52	14.42	7.82	1.55
SAGA	3.59	7.17	0.03	2.18	1.01	12.36	64.86	9.06	12.32	0.00	0.40
SAGB	3.09	8.84	0.00	2.99	0.52	18.36	50.19	16.14	13.92	0.20	0.19
SAGC	6.37	9.11	0.00	1.14	0.34	13.45	56.28	13.47	11.91	0.31	0.32
SAGD	3.14	11.63	0.16	1.99	1.57	17.48	53.17	11.02	12.20	0.00	0.69
SAGSP	4.31	10.93	2.59	6.09	1.67	10.55	63.19	1.96	8.62	0.00	1.99
SHANTY	4.31	15.43	0.00	0.45	0.22	17.55	60.31	1.80	7.80	8.44	0.34
SHEEPA	9.25	13.97	1.21	2.80	0.32	13.99	58.06	2.39	18.71	1.03	1.12
SHEEPB	12.63	10.48	0.18	7.37	0.29	12.39	51.72	6.50	22.23	2.43	5.51
SHEEPC	12.78	23.51	0.05	9.86	0.50	14.25	35.66	7.51	25.51	0.00	6.24
SPALD	0.00	16.92	0.48	0.00	0.04	12.63	63.11	6.73	9.46	1.02	0.00

Appendix 4 continued. Vegetation and ground cover (%) summaries for each plot.

PLOT	Sandberg bluegrass	Perennial Grass	Annual Grass	Perennial Forb	Annual Forb	Litter	Baroground & Rock	Moss & Crust	Wyo. Big sagebrush	Other Shrub	Tall Forb (≥18 cm)
SQUAWBU	3.55	19.15	0.03	4.95	0.10	12.23	55.55	4.83	10.08	1.33	0.79
SQUAWCR	2.25	18.13	2.19	0.53	3.64	14.63	59.25	1.42	7.91	1.05	0.66
STAR	3.40	7.44	0.00	7.55	1.23	16.66	60.03	3.96	18.98	1.73	5.02
STIPAHIL	3.88	8.96	0.03	1.96	0.54	12.71	66.26	5.99	14.25	0.00	0.92
TGIF	8.08	8.59	0.04	7.13	1.26	15.44	54.50	5.21	14.42	0.32	4.08
THEROCK	3.12	8.04	0.76	0.29	0.24	13.04	65.89	8.76	21.92	0.00	0.09
TOPPINA	2.30	12.04	0.00	6.09	0.84	10.53	65.19	3.34	15.62	0.00	2.10
TOPPINB	4.96	17.32	0.00	4.87	0.34	9.78	60.36	2.67	5.28	0.54	2.59
TOPPINC	3.43	20.32	0.00	3.63	0.25	14.34	55.71	2.82	14.28	0.00	2.60
TOPPIND	5.36	19.42	0.03	3.97	0.49	12.79	52.29	5.87	12.63	0.00	1.82
TOPPINE	5.93	9.81	0.02	6.31	0.53	13.06	57.62	6.95	10.43	0.00	1.85
TROUGHHA	8.15	12.77	0.09	2.82	0.52	17.54	47.56	10.82	12.53	3.86	0.91
TROUGHB	5.03	11.51	0.99	2.20	0.19	23.94	50.20	6.02	11.42	0.42	1.00
TROUGHHC	6.01	17.96	0.18	6.25	0.22	16.40	49.84	3.22	5.74	0.30	2.39
TROUGHHE	4.12	12.79	0.81	2.78	0.25	27.32	49.18	2.89	8.06	0.41	1.22
WASH	4.33	9.81	0.00	6.17	0.41	6.63	61.57	11.42	7.00	0.88	0.63
WILSONA	4.03	6.01	0.09	6.82	0.66	8.70	61.23	12.56	13.34	0.00	0.85
WILSONB	5.69	6.96	0.03	5.03	0.43	13.14	60.54	8.34	12.30	0.00	0.84
WINDYA	4.49	8.79	0.59	5.60	0.21	9.48	66.90	4.07	12.36	0.00	4.44
WINDYB	4.05	10.85	0.02	2.48	0.19	9.12	67.72	5.68	14.87	0.00	2.14
WINDYC	6.41	12.11	0.23	2.70	0.23	11.93	60.29	6.35	9.28	0.00	1.55
WINDYD	5.65	10.92	0.00	3.74	0.25	9.06	61.00	9.56	11.64	0.00	2.92