Vegetation Characteristics of Wyoming Big Sagebrush Communities Historically Seeded with Crested Wheatgrass in Northeastern Great Basin, USA

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VEGETATION CHARACTERISTICS OF WYOMING BIG SAGEBRUSH
COMMUNITIES HISTORICALLY SEEDED WITH CRESTED
WHEATGRASS IN NORTHEASTERN
GREAT BASIN, USA

by

Justin R. Williams

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Range Science

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah

2009
ABSTRACT

Vegetation Characteristics of Wyoming Big Sagebrush Communities Historically Seeded with Crested Wheatgrass in Northeastern Great Basin, USA

by

Justin R. Williams, Master of Science
Utah State University, 2009

Major Professor: Dr. Roger E. Banner
Department: Wildland Resources

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is one of the most commonly seeded grass species in the western United States and dominates thousands of hectares in the Great Basin. Although many degraded Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plant communities have been seeded with crested wheatgrass, successional pathways, influence of soil attributes, and cultivation history on the vegetation of these communities have not been fully characterized. I sought to identify community phases, vegetative differences, and soil attributes that explain variation among 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. All communities were more than 30 years old and had not experienced fire, or received subsequent chemical or mechanical treatments following their original seeding. Species richness, diversity, vegetation cover, and soil samples were measured in four 20 x 5 m intensive Modified Whittaker plots per community. Hierarchical clustering and principal component analysis of three indicator species
(crested wheatgrass, Sandberg bluegrass, and Wyoming big sagebrush) identified four distinct community phases. Community phase 1 was dominated by crested wheatgrass and had the lowest species richness and cover of big sagebrush. Phases 2 and 3 had the highest species richness and cover of native species. Phase 4 was dominated by big sagebrush and had the lowest cover of crested wheatgrass. Community phases differed significantly for soil texture, soil nitrogen, and ground cover characteristics. Bare soil was almost double on loam-textured soils and rock cover was higher on clay loam texture soils ($P < 0.05$) as well as native plant cover. Communities previously cropped occurred on more coarse-textured soils and had 6-fold lower native species cover and double exotic herbaceous and crested wheatgrass cover. Cropping occurred on favorable, low rock, fine-texture soils, the same soils that favor crested wheatgrass production and reduce resilience of native plant composition. Delineation of community phases provided a new, empirically based state-and-transition model, while the characterization of soil attributes and disturbance history provided information about feedback mechanisms influencing dominant species that delineate community phases and effect community structure. This information can be used to assist in the development of management strategies in crested wheatgrass seeded communities.

(99 pages)
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Justin R. Williams
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Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is an exotic grass that has been seeded on thousands of hectares in the Great Basin. These seeded communities represent one of the largest-scale land management manipulations within the sagebrush-steppe ecosystem. Pervasive overgrazing across this ecosystem diminished native herbaceous plant cover and promoted dense stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) and the opportunity for weed invasion (Young et al. 1999). In the early 1950s, large-scale preventative measures were taken to control the spread of the poisonous weed halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.) (Mathews 1986). Federal appropriations were granted to government agencies to prevent further expansion of halogeton and other weeds, improve forage potential, reduce fire frequency, and stabilize soil resources of these degraded landscapes (Blaisdell et al. 1982; Mathews 1986). Since the 1970s, crested wheatgrass has been planted on private and public lands in the Great Basin primarily following wildfires to maintain rangeland productivity, and reduce the spread of invasive annual species, including downy brome (*Bromus tectorum* L.), Russian thistle (*Salsola kali* L.), tumble mustard (*Sisymbrium altissimum* L.) and medusahead rye (*Taeniatherum caput-medusae* [L.] Nevski). Hundreds of articles were published in scientific journals between 1950 and 1980 on management implications of crested wheatgrass communities. The majority of these articles focused on methodologies to properly manage these communities for forage production while preventing sagebrush from reinvading. In our contemporary era of
rangeland management, emphasis has focused on stabilization and restoration of shrub-steppe communities. Current rangeland rehabilitation emphases include reducing wildfire frequency, improving species diversity, improving critical winter habitat for big game species, and protecting habitat for threatened and endangered wildlife species (Pellant and Lysne 2005).

Today, vast landscapes within the Great Basin contain or are dominated by crested wheatgrass. While these landscapes were stabilized and forage potential was improved by crested wheatgrass, these historic seedings have not been comprehensively characterized to determine their vegetative composition, structure, or functional attributes. Specifically, this extensive land-management treatment has not been adequately assessed in terms of the multiple interacting factors that determine vegetation attributes and successional trajectories. Assessing multiple interacting factors has aided in characterizing vegetation dynamics in short-grass prairie, Intermountain region mountain-meadow, salt-desert shrub, and southwest shrub ecosystems (Milchunas et al. 1989; Stohlgren et al. 1999; Beever et al. 2003; Milchunas 2006). Some studies have evaluated the role of singular factors controlling vegetation dynamics of crested wheatgrass seedings (Currie and Peterson 1966; McKell 1986; Angell 1997; Krzic et al. 2000) however, none consider the influence of multiple interacting factors across numerous locations or characterize cover components of established naturalized seedings older than thirty years. This project was designed to evaluate data collected from Wyoming big sagebrush communities historically seeded with crested wheatgrass to better understand successional processes, and formulate a comprehensive state-and-
transition model for these communities. Perhaps, these models can help identify opportunities to assess, monitor, and manage these ecosystems.

LITERATURE REVIEW

Brief history of Great Basin vegetation

The Intermountain Semi-desert and Desert Province Ecoregions as described by Bailey (1995) contain an area known as the Basin and Range or Great Basin, a high elevation, mountainous, cool desert (Irwin-Williams et al. 1990). This distinct land-area consists of many vegetation cover-types (Johnson 1989; Shiflet 1994; Young 1994). In particular, sagebrush-steppe cover types are characterized by a co-dominance of woody shrubs and herbaceous understory of bunchgrasses and forbs (West 1988). The common native species found today probably occurred in different abundance and composition before historic human-influenced disturbances.

Pre-settlement composition of vegetation is difficult to predict for many reasons. The first explorers in the Great Basin emphasized the dominance of sagebrush. Historical ecology confirms sagebrush dominance (Rogers 1982; Vale 1975); however, some locations may have been grass-dominated (Hull and Hull 1974). Kay (2007) suggests aboriginal burning was a dominant ecological force in sagebrush-steppe ecosystems, thus grass-dominated areas were more common if affected by aboriginal-mediated fire regimes. Variability in vegetation dominance in the Great Basin sagebrush-steppe has been attributed to dynamic variation in fire frequency, climate, and herbivory (Mack and Thompson 1982; Wright 1985; Knight 1994; Swetnam et al. 1999; Egan and Howell 2001; West and Yorks 2006).
Considerable evidence exists indicating that regardless of sagebrush dominance, native grass and forb abundance has drastically declined (West 1988; Johnson 1989). Since large herbivores were not present in numbers to adversely affect herbaceous species, the decline in abundance has been attributed to poor grazing tolerance of native species associated with the absence of intensive ungulate herbivory prior to European settlement (Mack and Thompson 1982). Wildfires did occur; however, herbaceous species have the potential to readily re-grow while sagebrush does not (Wright 1985). Thus, wildfire functioned as an ecosystem driver to determine relative abundances of sagebrush and herbaceous cover (Kay 1960; Harniss and Murray 1973; Wright 1985; Monsen 1994; Bork et al. 1998).

Fire frequency within sagebrush-steppe ecosystems has also changed considerably since European settlement. Changes in fire frequency were initiated as a consequence of annual weeds replacing native herbaceous species (Young and Evans 1973; Monsen 1994). Foremost among these annual weeds are downy brome and medusahead rye, which produce fine-fuels that carry fire more readily than native species (Young and Evans 1973; Whisenant 1990). The spread and dominance of annual weeds fueled larger wildfires and perpetuated further expansion of annual weed infestations. Introduction of livestock grazing and annual weed-mediated changes in wildfire frequency greatly reduced the forage potential of sagebrush-steppe (Griffiths 1903; Pickford 1932). Consequently, land management attempted to end the misuse of sagebrush-steppe rangelands in the early 1900s (Stoddart and Smith 1955); however, overgrazing and wildfire continued to alter this ecosystem well into the twentieth century because of the demand for livestock production for World Wars I and II (Young 1994; Chatterton and
Young 2002). In this era, improving the forage potential of these lands was the primary goal of resource managers (Young and Evans 1986).

**Introduction of crested wheatgrass into the Great Basin**

Revegetation became an important component of restoration efforts of damaged rangelands in the Great Basin. Efforts to revegetate rangelands began with attempts to establish native and introduced plant species onto degraded sites (Monsen 2004). Identifying forage grasses to improve rangeland productivity was the research emphasis of P. B. Kennedy and A. W. Sampson (Chatterton and Young 2002). These early researchers found exotic forage grasses were very successful, however, early efforts to establish native species were not as successful (Monsen 2004). Many exotic grasses, including crested wheatgrass performed better than the available native species, which became the “gold standard” to use on damaged shrub-steppe and sagebrush rangelands (Young and McKenzie 1982). Crested wheatgrass was first introduced into the Northern Great Plains in 1898 and later promoted as a successful revegetation species suitable for the needs of land managers (Dillman 1946; Rogler and Lorenz 1983; Young and Evans 1986). The first seeding evaluations in the northern Great Basin and Snake River Plain were made in the early 1930s (Hull and Klomp 1966). Reclamation of abandoned dryland farms and unproductive sagebrush pastures on private and public land prompted government researchers to publish bulletins on how to reseed these rangelands in Nevada, Idaho, and Utah in the early 1940s (Young and Evans 1986; Pelland and Lysne 2005). Less productive sagebrush-steppe grazing areas were plowed and seeded with crested wheatgrass to increase forage production, promote the rehabilitation of degraded
rangelands, and increase meat production to support the World War II effort (Young and Evans 1986). Eventually, the use of crested wheatgrass greatly expanded in 1952 with the Halogeton Control Act, a program designed to stop the spread of the poisonous, annual weed halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.) (Mathews 1986). Seeding crested wheatgrass throughout the Great Basin and beyond helped control halogeton (Young and Evans 1986).

Establishing crested wheatgrass required modifying traditional agricultural techniques to fit a new set of obstacles associated with seeding rough rangelands. Developing the rangeland drill and brushland plow effectively allowed sagebrush removal and large seedings over rough terrain (Young and McKenzie 1982). Large-scale seedings continued until the 1970s, when crested wheatgrass became the focus of controversy (Chatterton and Young 2002; Pellant and Lysne 2005). This controversy stemmed from the perception that crested wheatgrass may be responsible for low quality wildlife habitat and low recruitment of native plant diversity (Wilson 1989; Dobkin and Sauder 2004). Thus, federal agencies were encouraged to use native species in new seeding projects when feasible, depending on availability, cost, and potential for establishment (Pellant et al. 2004; Pellant and Lysne 2005). Crested wheatgrass is still used in large-scale seedings on public lands, but it is now a component of a more diverse seed mix that includes native species (Pellant and Lysne 2005). The underlying issue today is that crested wheatgrass exists on millions of hectares of public and private rangelands and is a naturalized vegetation component of where it was established in the past.
As the need to reclaim degraded rangelands increased, the production of crested wheatgrass seed also increased (Sharp 1986). Thus, in addition to being easier to establish than native grasses, high seed availability also led to its preference for rangeland seedings. Good seedling vigor makes crested wheatgrass ideal for reclamation because it is very competitive with slower growing species, is drought tolerant, and has an efficient nutrient acquiring root system (Eissenstat and Caldwell 1988; Caldwell et al. 1991; Bakker and Wilson 2001). In addition, crested wheatgrass is competitive with weedy species and resists downy brome better than native species, because it germinates earlier and grows more rapidly at colder temperatures (Aguirre and Johnson 1991; Chatterton and Harrison 2003). It is long-lived and perpetuates stable populations primarily by good seed production (Marlette and Anderson 1986). Forage production is two-fold greater than native range in shrub-steppe ecosystems with limited precipitation capabilities (Springfield et al. 1967; Laycock and Conrad 1981; Hart et al. 1983; Gade and Provenza 1986; Angell et al. 1990; Ganskopp et al. 1997). Crested wheatgrass is also known to have superior drought tolerance (Caldwell and Richards 1986; Sharp et al. 1992) and can persist under drought conditions in semi-arid environments (Currie and Peterson 1966; Busso et al. 1990). In general, crested wheatgrass can withstand heavy grazing (Cook et al. 1958; Caldwell et al. 1981; Laycock and Conrad 1981; Sharp 1986; Angell 1997) with some limitations (Sharp 1970). Because crested wheatgrass evolved with ungulate grazing pressure, it is well adapted to higher utilization levels than native Great Basin grasses (Sharp 1986). Crested wheatgrass can withstand intense biomass removal because of its ability to reestablish pre-defoliation leaf area and high compensatory photosynthesis (Frischknecht and Harris 1968; Olsen and Richards 1988).
**Succession in communities seeded with crested wheatgrass**

Early research on crested wheatgrass management focused on grazing and fire as well as other mechanical and chemical treatments to maintain crested wheatgrass productivity and dominance (Mueggler and Blaisdell 1958; Klomp and Hull 1972; McLean and Van Ryswyk 1973; Hull 1974; Evans and Young 1978). Although crested wheatgrass out-performs native grasses in reducing shrub seedling invasion (Blaisdell 1949; Frischnecht and Bleak 1957; Schuman et al. 1982), without fire, chemical, or mechanical treatments, sagebrush reinvades over time (Frischknecht and Bleak 1957; Hull and Klomp 1966). A review of these management activities is a necessary and preliminary step to determine the potential of seedlings to continue as stable crested wheatgrass stands or be reinvaded by native sagebrush-steppe species from adjacent plant communities (Johnson and Payne 1968).

Livestock grazing practices, including intensity, duration, season, and animal type, impact plant succession in communities seeded with crested wheatgrass (Pieper 1994; Holechek et al. 1995). Crested wheatgrass dominance is maintained, and sagebrush encroachment is reduced, by heavy autumn grazing more so than spring grazing (Frischknecht and Harris 1968; Robertson et al. 1970; Hull and Klomp 1974; Laycock and Conrad 1981). In addition, sheep versus cattle grazing of crested wheatgrass reduces shrub encroachment (Bleak and Plummer 1954; Laycock and Conrad 1981; Blaisdell et al. 1982). Livestock grazing can also directly reduce shrub invasion by trampling seedlings (Owens and Norton 1992). Conversely, livestock grazing practices can also promote sagebrush reinvasion, particularly prolonged spring grazing during drought
(Busso and Richards 1995). Overutilization of crested wheatgrass through high intensity, long-duration grazing reduces grass productivity and enhances seedling survival of other species including sagebrush (Salihi and Norton 1987; Angell 1997). Grazing crested wheatgrass in the spring reduces its dominance and may allow invasion of brush species (Robertson et al. 1970; Laycock and Conrad 1981; Olsen and Richards 1988). However, even when grazing is used to maintain crested wheatgrass dominance, periodic treatments to reduce sagebrush are necessary (Astroth and Frischknecht 1984; Torell 1986).

Management activities that directly kill shrub and herbaceous dicotyledonous species have obvious impacts on maintaining crested wheatgrass dominance. However, similar to grazing, the absence of fire and brush removal treatments (chemical and mechanical) allows crested wheatgrass seedlings to be reinvaded by native sagebrush-steppe species from adjacent plant communities. Prescribed fire perpetuates crested wheatgrass dominance because herbaceous species have high post-burn vigor and productivity, whereas sagebrush is killed (Kay 1960; Lodge 1960; Harniss and Murray 1973; Wright 1985). Mechanical treatments, including plowing, disking, chaining, mowing, and the use of pipe harrows, rails and cables, effectively control shrub abundance and density and facilitate herbaceous dominance (Mueggler and Blaisdell 1958; Lodge 1960; Pechanec et al. 1965; Parker 1979; Blaisdell et al. 1982; Young and McKenzie 1982; Wambolt and Payne 1986; Vallentine 1989). Finally, chemical control with the herbicides 2, 4-D and tebuthiuron successfully reduce shrub density and increases crested wheatgrass dominance (Johnson and Payne 1968; Eckert et al. 1972; Evans et al. 1979; Astroth and Frischknecht 1984; Holechek et al. 1995; Cox and Anderson 2004; Pellant and Lysne 2005). The effectiveness of these treatments to
maintain crested wheatgrass dominance is also determined by their season of application (Evans and Young 1978; Blaisdell et al. 1982).

Non-management factors may also indirectly influence successional trajectories in communities seeded with crested wheatgrass. First, the resilience and dominance of crested wheatgrass seedings depends on how well the initial seeding establishes (Hull 1974). Variability in seedbed preparation, including weed and shrub control, determines soil moisture retention and the competitive ability of crested wheatgrass seedlings (Mueggler and Blaisdell 1958; Klomp and Hull 1972; McLean and Van Ryswyk 1973; Hull 1974; Vallentine 1989; Holechek et al. 1995). Second, soil properties may be a good predictor of successional trajectories because soil nutrients, aggregate stability, bulk density, soil penetration resistance, and water infiltration are known to remain stable under long-term livestock grazing in crested wheatgrass seedings compared to adjacent native-dominated rangeland (Krzic et al. 2000). Third, variability in seasonal precipitation and topography are not only the most influential factors determining vegetation dynamics in sagebrush-steppe plant communities (Cook and Irwin 1992; West and Yorks 2006), but may also interact with management activities to determine vegetation status of crested wheatgrass seedings (West 1988; Sharp et al. 1992). However, management activities that remove woody and herbaceous dicotyledonous species obscure the role of indirect factors in determining secondary succession within seeded communities because of the obvious impact shrub removal has on maintaining crested wheatgrass dominance.

A practical approach to objectively differentiate between and understand the potential triggers of secondary succession is to evaluate these multiple interacting factors
in historically seeded Wyoming big sagebrush communities that have not experienced
fire and shrub removal. In the absence of management activities that acutely reestablish
crested wheatgrass dominance, attention can be focused on livestock grazing, initial
seeding establishment success, soil properties, climate, and topography. This approach
has been used to describe vegetation dynamics of many North American plant
communities, i.e., subtropical savanna (Archer and Smeins 1991), tallgrass prairie
(Fuhlendorf et al. 2001), central Great Plains prairie (Cook and Irwin 1992; Guretzky et
al. 2005), shortgrass-steppe (Milchunas and Lauenroth 1993), sagebrush-steppe
(Anderson and Inouye 2001), salt desert shrubland (Young 1994), and Chihuahuan desert
(Peters et al. 2004). Thus, I reasoned this approach has the potential to define
successional phases and possible pathways among plant communities, clarify the
importance of multiple interacting factors, and provide insights into management
opportunities to satisfy contemporary and future rangeland management goals within
crested wheatgrass seeded Wyoming big sagebrush plant communities.

State-and-transition models in seeded communities

Evaluation of ecosystem dynamics and methods to establish management
objectives on rangelands have been assisted with the development of models that explain
successional pathways and alternative stable states on varied ecological sites (Westoby et
al. 1989; Friedel 1991; Laycock 1991; Tausch et al. 1993; Bestelmeyer et al. 2003;
Stringham et al. 2003). These models assist understanding the dynamics of community
phases (Bestelmeyer 2006; Briske et al. 2008). A community phase is a period or episode
in time of the species present in the community. Phases are measured by the dominant
species taking up the most space or cover and can change depending on disturbance. Some attempts to characterize succession in Wyoming big sagebrush communities were useful for relating vegetation changes to successional phases of different states (Tueller and Platou 1991). However, these focused primarily on threshold-exceeding changes and not within-state movements or resilience of alternative states (West 2000; Briske et al. 2008). Empirical characterizations of Wyoming big sagebrush communities have emerged with the adoption of the state-and transition/opportunistic management model (Westoby et al. 1989; Briske et al. 2005). The ability to identify, assess, and monitor community changes will assist with developing resilience-based management strategies that anticipate ecosystem changes (Briske et al. 2008).

**Implications**

Crested wheatgrass was initially adopted to restore the productivity of depleted rangelands. However, there are concerns about low diversity and the long-term effects of introduced plants on native landscapes, in particular, wildlife habitat, soil quality, and ability to resist invasive plants (Holechek 1981; Wilson 1989; Dormaar et al. 1995; Dobkin and Sauder 2004). Many of these concerns are based on the lack of research on older crested wheatgrass seedings (> 30 years). Therefore, addressing the following questions may help managers make important decisions for future management. Do Wyoming big sagebrush communities historically seeded with crested wheatgrass remain resilient as a singular community phase, or do multiple phases develop in the absence of obvious factors that remove sagebrush? What is the variability in species abundance and diversity in old crested wheatgrass seedings and are they functionally different than
native sagebrush-steppe rangelands managed similarly? Is the perception of low plant diversity in crested wheatgrass seedings a myth perpetuated by obvious management activities and pre-seeding soil attributes that favor crested wheatgrass dominance? Is resilience of crested wheatgrass caused by seed limitation of native species or competitive exclusion of seeds that arrive? What is the role of grazing on plant species diversity, relative to the factors of soil and climate? These questions can be addressed through the practical approach of evaluating the relationships between multiple interacting factors, i.e., vegetation, grazing history, soil properties, climate, and topography on historically seeded Wyoming big sagebrush seedings that have not experienced fire or other mechanical and chemical treatments. Thus, my research may help define how these multiple interacting factors determine successional trajectories and provide insights into management options to satisfy contemporary and future rangeland management activities within Wyoming big sagebrush communities seeded with crested wheatgrass.

**OBJECTIVES**

After locating 35 Wyoming big sagebrush plant communities in the northeastern Great Basin that had been seeded with crested wheatgrass at least 30 or more years ago, I evaluated and characterized vegetation to delineate community phases when successional pathways were not influenced by management treatments and wildfire. Further characterization focused on soil attributes, ground cover, and disturbance history most likely correlated to vegetation patterns as well as climate or general topography features. The objectives of my first study were to 1) identify indicator species that describe the
most variation between communities, 2) determine if distinct phases exist in these communities, and 3) develop a more comprehensive and empirically based state-and-transition model for crested wheatgrass seeded Wyoming big sagebrush communities.

The objectives of my second study were to 1) identify the soil and ground cover attributes related to variation in community phase classification, and 2) characterize influence of soil texture, cultivation history, elevation, and topography on vegetation and soil attributes in Wyoming big sagebrush communities historically seeded with crested wheatgrass.

LITERATURE CITED


CHAPTER 2

DELINEATING PHASES OF WYOMING BIG SAGEBRUSH COMMUNITIES
HISTORICALLY SEEDED WITH CRESTED WHEATGRASS

ABSTRACT

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is one of the most commonly seeded exotic species in the western United States, particularly the Great Basin. Although many degraded Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) plant communities have been seeded with crested wheatgrass during rehabilitation efforts, successional pathways of these communities have not been characterized. I sought to identify community phases and vegetative factors that explain the variation among 35 seeded Wyoming big sagebrush communities in the northeastern Great Basin. All communities were more than 30 years old and had not experienced fire, or received subsequent chemical or mechanical treatments following their original seeding. Species richness, diversity, and cover of vegetation were measured in four 20 x 5 m intensive Modified Whittaker plots per community. Hierarchical clustering and principal component analysis of three indicator species identified four distinct phases in these communities. Community phase 1 was dominated by crested wheatgrass and had the lowest species richness and cover of big sagebrush. Phases 2 and 3 had the highest species richness and cover of native species. Phase 4 was dominated by big sagebrush and had the lowest cover of crested wheatgrass. Delineation of community phases provides a new, empirically based state-and-transition model, and will assist with developing management strategies for seeded Wyoming big sagebrush communities.
INTRODUCTION

Prior to the arrival of Europeans into the Great Basin, Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis Beetle & Young) plant communities existed as a dynamic balance of co-dominance between sagebrush and native perennial bunchgrasses (West 1988). Wildfire occurred infrequently, but may have been a common tool used by Native Americans (Mensing et al. 2006; Kay 2007). Consequently, Wyoming big sagebrush ecosystems were arranged across the landscape at variable community phases depending on climate, topography, soils, and disturbance regime (West 1988; Davies et al. 2006, 2007; West and Yorks 2006; Benkobi et al. 2007). New community phases appeared with the introduction of pervasive heavy livestock grazing, invasion by exotic annual species, and seeding with crested wheatgrass (Agropyron cristatum [L.] Gaertn.) (Young et al. 1999). Succession models for big sagebrush communities recognize community phases within vegetation states and describe potential management opportunities for transitions between and within states (Laycock 1991). Certain transitions, including invasion by exotic annual species and seeding with crested wheatgrass, are considered irreversible because vegetation and soils are altered in ways that biotic and possibly abiotic thresholds are crossed (Whisenant 1990; Friedel 1991; Stringham et al. 2003). However, these models are primarily conceptual and lack detailed empirical information about community phases and threshold indicators to effectively bridge the gap between theory and application (Groffman et al. 2006). Also, detailed timelines for transitions are difficult to predict and cannot be determined under management and monitoring methods with consistent accuracy. Consequently, land
managers are limited in their ability to develop management strategies that promote desirable changes in these community phases.

Empirical characterizations of Wyoming big sagebrush communities have emerged with the adoption of the state-and-transition/opportunistic management models for rangeland ecosystems (Westoby et al. 1989; Briske et al. 2005). For example, four to five community phases have been delineated for intact, late-seral ecosystems based on cover percentages of important indicator species and other environmental characteristics (McAdoo 1986; Davies et al. 2006; Benkobi et al. 2007). Two community phases have been characterized for communities seeded with crested wheatgrass using species cover (Allen-Diaz and Bartolome 1998), while communities heavily invaded by exotic annual species are typically delineated into one vegetation state. Thus, identifying indicator species is appealing because it provides a basis to monitor and classify vegetation characteristics and soundly evaluate management alternatives within state and transition models.

Wyoming big sagebrush communities were historically seeded with crested wheatgrass to improve forage potential and conserve soil resources because of its ease of establishment, high grazing and drought tolerance, and because seed of native species was unavailable (Blaisdell et al. 1982; Mathews 1986; Salihi and Norton 1987). Thousands of hectares of Wyoming big sagebrush communities have been seeded since the 1930s throughout the Great Basin, Snake River Plain, and the Columbia River Plateau (Young and Evans 1986). The largest example of this practice was associated with the Halogeton Control Act of 1952, wherein federal funding was granted to management agencies to plow large expanses of degraded Wyoming big sagebrush communities in the
eastern Great Basin and seed crested wheatgrass to prevent the spread of the invasive species *Halogeton glomeratus* (M. Bieb.) C.A. Mey. (Sharp et al. 1992; Young and Evans 1986).

Seeded communities are typically dominated by crested wheatgrass in the early stages of succession with variable reestablishment of sagebrush and herbaceous forbs in later stages depending on the disturbance regime (Frischknecht and Bleak 1957; Hull and Klomp 1966; Rittenhouse and Sneva 1976). Many seeded communities were actively managed with mechanical and chemical treatments to kill sagebrush and other undesired shrubs and sustain high forage productivity of crested wheatgrass plants (Blaisdell et al. 1982). These management treatments represent a fairly obvious influence on the succession of Wyoming big sagebrush communities, as natural succession is halted, and crested wheatgrass often exists as a monoculture (Hull and Klomp 1966; West et al. 1979). Management treatments and wildfire events have long-lasting effects on sagebrush communities because they may cause local extinction of native species from the seed bank (Marlette and Anderson 1986; Pyke 1987; Anderson and Inouye 2001) and confound an objective interpretation of natural succession. Fortunately, many seeded communities were spared subsequent management treatments and have not experienced wildfire, which provides an ideal opportunity to evaluate how natural succession proceeds uninhibited by confounding factors across disparate landscapes and possibly clarify the processes responsible for the formation of community phases. Current state and transition models for Wyoming big sagebrush communities place seeded communities into a separate state with two phases (i.e., crested wheatgrass and crested wheatgrass re-colonized by big sagebrush) (NRCS 2008a). The current model suggests
that the first phase can transition to the second in the absence of fire, and the second reverts to the first with fire. While this interpretation may be appropriate for communities that have experienced management treatments and wildfire, it does not fully describe the potential successional pathways in the absence of confounding factors, and does not lend itself to interpreting these pathways in relation to environmental factors (Krzic et al. 2000). Moreover, reliable values for dominant indicator species will help develop a more contemporary state and transition model for monitoring and management activities.

Research and land management agencies emphasize developing strategies to improve native plant diversity, forage production, and wildlife habitat of Wyoming big sagebrush communities (Pellant and Lysne 2005). Communities seeded with crested wheatgrass are an attractive setting to incorporate the principles of successional management (Kruger-Mangold et al. 2006) because they are less prone to wildfire and annual grass invasion, and they respond in a predictable manner to livestock grazing and management treatments (Frischknecht and Bleak 1957; Hull and Klomp 1966; Blaisdell et al. 1982). In addition, recent emphasis has been placed on developing strategies to diversify seeded communities (Pellant and Lysne 2005), essentially using them as potential transitions to community phases with abundant herbaceous cover and greater structural heterogeneity (Cox and Anderson 2004; Fansler 2007). Late-seral seeded communities may therefore resemble the structure of late-seral native Wyoming big sagebrush communities, however, their function are likely drastically different because of fundamental differences in response to grazing and wildfire.

I located 35 Wyoming big sagebrush plant communities in the Northeastern Great Basin that were seeded with crested wheatgrass at least 30 or more years ago to
characterize vegetation and delineate phases when successional pathways were not confounded by management treatments and wildfire. My objectives were to 1) identify indicator species that describe the most variation between communities, 2) determine if distinct phases exist in these communities, and 3) develop a more comprehensive and empirically based state-and-transition model for Wyoming big sagebrush communities seeded with crested wheatgrass. A thorough characterization of the vegetation of seeded communities may reveal a broader understanding of successional management opportunities.

MATERIALS AND METHODS

Selection and description of communities

A total of 35 Wyoming big sagebrush communities seeded with crested wheatgrass were selected for this study. Communities were located on public lands administered by Bureau of Land Management (BLM) field offices in Cassia and Oneida counties in Idaho, Elko county Nevada, and Box Elder and Tooele counties in Utah (Figure 2-1). Communities met the following criteria: 1) successful initial establishment of crested wheatgrass, 2) prescribed and natural fire have not occurred since seeding, 3) chemical and or mechanical shrub removal treatments have not occurred since seeding, and 4) seedings were more than 30 years old. Each community was visited to validate criteria before inclusion in the study. Communities were primarily located in the northeastern Great Basin, a region central to seeding efforts associated with the Halogeton Control Act of 1952.
Elevations of communities ranged from 1380-1788 meters above sea level with most occurring on similar terrain, typical of Great Basin Wyoming big sagebrush habitat (West 1988). Mean average annual precipitation (1972 to 2007) for communities ranged from 178 to 382 mm. Precipitation primarily occurs as winter snow and spring rain (WRCC 2008). Regional precipitation for the 2006-2007 growing season (1 October to 30 September) was approximately 50% of the 35-year average (Figure 2-2). All communities are currently, and have been, grazed by livestock since the late-1800s. Communities occurred on soils typical of Wyoming big sagebrush ecosystems with the majority being Aridisols and Mollisols, but there are some Entisols and Inceptisols (Table A-1).

**Vegetation sampling**

Within each community, four 20 x 5 m plots were established at least 200 meters from fences, roads, water improvements, cultural resources, and landscape disturbances. Plots were also placed to avoid rock outcrops, bottom of washes, and steep slopes. Macro-topographic heterogeneity among plots was expected and could not be avoided.

Plots were an intensive version of the Modified-Whittaker plot (Stohlgren et al. 1995), oriented by magnetic north-south bearings. Modified-Whittaker plots are used to assess plant communities at multiple scales. The intensive version is used when more plots are needed across the landscape to facilitate better coverage of environmental gradients and for locating rare species. Modified-Whittaker plots are most efficient because they detect the greatest number of species per unit of sampling effort and provide data at different spatial scales (Leis et al. 2003). Plots contained one 10 m² (5 x 2 m) and
four 1 m² (2 x 0.5 m) subplots nested within the 100 m² plot (Figure 2-3). Plots were sampled during peak herbaceous productivity, corresponding to the period between May and June 2007. Percentage vegetation canopy cover for each plant species rooted in plot and ground cover category (bare ground, rock, litter, and crypto-biotic crust) were visually estimated within each 1-m² subplot following procedures of Stohlgren et al. (1995). Cover data was collected by one individual for all sites to minimize bias. Species richness was determined by totaling the number of different plant species present in 100-m² plots. Species richness data from the 1 and 10 m² (5 x 2 m) plots were not used in this study. Shannon-Weiner diversity (H’) was calculated from plant cover in 1 m² subplots using the following equation: $H' = -\sum p_i \ln p_i$. Nomenclature for all plant species followed NRCS (2008b) PLANTS database.

**Statistical analyses**

Cover data were square root transformed to improve normality of many variables. However, normality could only be attained for crested wheatgrass, Sandberg bluegrass (*Poa secunda* J. Presl), and Wyoming big sagebrush (indicator species). Thus, all species were combined according to their respective growth form (herbaceous vs. shrub) and origin (native vs. exotic) to create groups that met the normality assumptions of analysis of variance (ANOVA). Indicator species were analyzed using a hierarchical clustering procedure, which grouped the 35 sites into four distinct clusters (phases). Indicator species were also analyzed with principal components analysis (PCA) to synthesize compound axes (1 and 2) that explain the highest proportion of the original total variance (McCune and Grace 2002). The PCA analysis also weighed the contribution of axes and
indicator species to differences between sites. Position of sites along these principal axes displayed cover of indicator species according to the phases generated by hierarchical clustering.

Analysis of variance (ANOVA) was used to analyze indicator species cover, species richness, species diversity, and cover of grouped species for differences between the four phases. For significant ANOVA models, means were compared with Fisher’s LSD tests. All analyses, including hierarchical clustering, PCA, and ANOVA were conducted with JMP 5.1 (SAS Institute) using $P < 0.05$ to determine significance. Because cover data for most species could not be normalized, we generated descriptive statistics (mean, median, minimum, maximum, and standard error) for individual species.

**RESULTS**

**Dominant indicator species**

Of the 51 plant species observed at the 35 communities, only crested wheatgrass (15%), Sandberg bluegrass (4%) and Wyoming big sagebrush (8%) had mean cover percentages greater than 1.5 percent (Tables A-2, A-3, and A-4). Canopy cover of indicator species explained over 85% of the variation of the PCA axes (Table 2-1). Axis 1 shows positive weightings for Wyoming big sagebrush and Sandberg bluegrass, and a negative weighting for crested wheatgrass. In contrast, Axis 2 had positive weightings for the two grasses, and a negative weighting for Wyoming big sagebrush.
Community phases

Hierarchical clustering of the three indicator species identified four distinct phases among the 35 communities. Phases also clustered when communities were plotted using PCA axes 1 and 2, and indicator species cover varied with phase (Figure 2-4). Crested wheatgrass cover in phase 1 was 7- and 20-fold greater than Sandberg bluegrass and Wyoming big sagebrush, respectively (Figure 2-5). In contrast, crested wheatgrass cover in phases 2 and 3 was roughly half that of phase 1, and was below 5% in phase 4. Sandberg bluegrass cover equaled crested wheatgrass in phase 2, and was lowest in phases 1 and 4. Wyoming big sagebrush cover was lowest in phases 1 and 2, yet equaled crested wheatgrass cover in phase 3. Wyoming big sagebrush cover was more than double both grass species cover in phase 4.

Herbaceous cover dominated vegetation in phases 1 and 2, while shrub cover dominated phases 3 and 4 (Figure 2-6). Wyoming big sagebrush made up most of the shrub cover (Figure 2-6), however, a few communities had higher contributing shrub cover by other shrub species, inflating the mean total shrub cover (Table A-3). Native herbaceous species cover mirrored cover of Sandberg bluegrass over the phases (Figure 2-7). Similarly, exotic species cover generally followed the pattern of crested wheatgrass cover over the phases, characterized by the significantly highest and lowest cover in phases 1 and 4, respectively. Species richness was significantly higher in phase 2 and lowest in phase 1 (Table 2-2). Diversity ($H'$) was highest in phases 2 and 3, corresponding with increasing native species cover of Sandberg bluegrass and Wyoming big sagebrush.
DISCUSSION

Possibly the most robust observation from my study is that Wyoming big sagebrush communities historically seeded with crested wheatgrass can potentially experience four distinct successional pathways (Figure 2-8). A common perception is that seeded communities remain in phase 1 because crested wheatgrass effectively prevents the establishment of many native herbaceous plants and may actually impede restoration of species diversity on the site (Bunting et al. 2003). While this is certainly the case for communities that experience wildfire, or other prescribed management treatments that promote crested wheatgrass dominance, my assessment indicates that crested wheatgrass dominance may also occur in the absence of these treatments. High crested wheatgrass cover and minimal sagebrush and Sandberg bluegrass cover are biotic indicators that maintain the resilience of community phase 1. Resilience can be developed by wildfire and management activities that abruptly remove re-invading sagebrush, re-enforcing crested wheatgrass dominance. High crested wheatgrass cover and shrub removal establish a negative feedback whereby tight nutrient cycling and competition for soil water and nutrients promote the ecological resilience of phase 1 (Bilbrough et al. 1997; Chen and Stark 2000). The absence of native species and the proportional dominance of crested wheatgrass in soil seed banks also serve as indicators of the feedbacks responsible for this community phase to remain fairly stable (Marlette and Anderson 1986; Anderson and Inouye 2001). Interestingly, the same feedback mechanisms that prevent the accumulation of greater species diversity in phase 1 may also have the positive aspect of
being resistant to annual grass invasion even when crested wheatgrass is heavily
defoliated (Sheley et al. 2008).

Crested wheatgrass is much more tolerant of heavy grazing than most native
species and can withstand higher levels of utilization (Bleak and Plummer 1954; Laycock
and Conrad 1981). Thus, resilience of phase 1 can be reduced by repetitive heavy spring
grazing because it directly impacts crested wheatgrass production and creates
opportunities for sagebrush to establish (Frischknecht and Bleak 1957; Hull and Klomp
1966; Harris et al. 1968; Rittenhouse and Sneva 1976). However, because the
communities evaluated in my study had comparable grazing histories, the emergence of
phases 2-4, is likely associated with grazing interacting with edaphic or climatic
attributes. Evidence for this interpretation is based on the fact that 13 of the communities
were resilient to change and remained in phase 1 while the other three communities
experienced phase shifts to higher diversity and co-dominance by big sagebrush under
essentially the same disturbance regime since being seeded with crested wheatgrass.
Thus, my results suggest that grazing pressure alone is not responsible for the observation
of four distinct community phases, and that linear shifts between phases cannot be
predicted by grazing alone and is more likely a combination of other factors (Tueller and

Ecological theory suggests that community phase shifts occur when the negative
feedbacks that enhance resilience diminish while positive feedbacks that promote change
increase (Briske et al. 2008). Applying this theory to my study, it appears that the
feedbacks that enhance the continued dominance of crested wheatgrass have diminished
in community phases 2-4, providing an opportunity for native species to reinvade. While
it is too speculative to assume that the community phases developed in a linear fashion
(i.e., phase 2 => 3, then 4), the assembly and/or emergence of phases 2-4 can be
elucidated by addressing potential factors that reduce crested wheatgrass cover and
provide opportunities for native grass and sagebrush establishment.

Community phase development can occur based on multiple-interacting factors
such as pre-existing edaphic properties, distance from seed sources, shifts in precipitation
patterns, and exaggerated grazing practices (Bestelmeyer 2006). These factors in
combination, can promote an overload of positive feedbacks, enhancing plant community
response and influence to reduced crested wheatgrass competition. The outcome of these
positive feedbacks is the reduction of established crested wheatgrass cover and negative
feedback response that promotes resilience of native grass or sagebrush dominated
communities (McWilliams and Van Cleave 1960). An example of a possible phase shift
from 1 to 4 in a relative short period of time is crested wheatgrass being seeded and
successfully establishing during an above average precipitation year. Although the
crested wheatgrass established, the pre-existing soil properties are not favorable to
grasses (i.e., coarse texture), corresponding to Davies et al. (2007) findings that bunch
grasses are more productive on finer textured soils. Proximity to a productive sagebrush
seed source can increase the rate of reinvasion (Marlette and Anderson 1986). In
subsequent years following seeding, prolonged drought favors emerging sagebrush
seedlings, capable of utilizing water in the deeper, coarse soils (Hull and Klomp 1966).
Enhanced by high stocking rates, grazing pressure on crested wheatgrass has a negative
feedback response for invading sagebrush (Holechek and Stephenson 1983; Angell 1997;
Anderson and Inouye 2001). Over time, sagebrush quickly dominates and a continued
negative feedback increases the phase resilience for sagebrush while reducing the resilience of the crested wheatgrass component (Hull and Klomp 1966; West and Yorks 2006). Together, in combination, multiple-interacting factors are influencing the composition in all phases. Assessing and monitoring the plant community’s ecological triggers can help determine reversible feedback switches between phases.

The critical role of dominant species in determining vegetation structure, successional patterns, invasibility, and nutrient cycling is well recognized (Seabloom et al. 2003; Emery and Gross 2006). By virtue of their large biomass, high density, or extensive cover (or all), ecosystem dominants also provide the context within which other species persist (Denslow and Hughes 2004). Not surprisingly, the three dominant species (crested wheatgrass, big sagebrush, and Sandberg bluegrass) explained 85% of the variation among the 35 plant communities. As ecosystem drivers, the dominant species affecting species diversity, structural composition, nutrient cycling, and biomass production, cause possible stability among communities as they interact with soils, climate, and the prevailing disturbance regime to determine the functional status of community processes (Stringham et al. 2003). These dominant species may function as ideal indicators for delineating community phases of other sites and determining ecosystem status in a monitoring program. According to Havstad and Herrick (2003), effective long-term monitoring techniques should be based on valid plant, soil, and functional indicators that can help initiate adaptive management protocols. My identification of indicator plant species and associated community phases could be combined with other robust indicators of rangeland health to determine rangeland health
and develop more accurate state-and-transition models (STM) for Wyoming big sagebrush communities seeded with crested wheatgrass (Pyke et al. 2002).

The phases I identified for Wyoming big sagebrush communities seeded with crested wheatgrass have not been previously identified or incorporated into the current STM. The Natural Resource Conservation Service (NRCS 2008a) ecological site description for semi-desert loam, Wyoming big sagebrush (Major Land Resource Area D28A, [028AY220UT]) could be expanded to include this new delineation (Figure 2-8). In this model, seeded communities arise when an ecological threshold is crossed through the event of a rangeland seeding. Although, I did not seek to measure the factors responsible for community phase shifts, future research to determine processes and strategies to do so may provide identifiable, interrelated ecological and management events that contribute to ecosystem resilience monitoring and decision making (Briske et al. 2008). While it is obvious that a return to phase 1 from phases 2-4 would be caused by fire, herbicide, or mechanical disturbance, I am reluctant to suggest that seeded communities will ever resemble the potential natural community. In contrast, it is quite clear that phase 4 of seeded communities and the sagebrush-dominated state in the NRCS model are similar in sagebrush dominance and the general lack of herbaceous understory cover. For this reason, I suggest that phase 4 is the community at risk, because the understory will not return by relaxing grazing, and it is the most susceptible phase to annual grass invasion and conversion to an annual dominated state following a wildfire event.
CONCLUSION

Although the long-term successional characteristics of ecosystems may become stable over long periods, they are continually changing by multiple disturbances (Ott et al. 2003). This study provides an expanded model for stakeholders to consider for seeded communities and suggests some potential options to manage for resilience of specific community phases. Here, I suggest that plant communities should be delineated based on dominant species and reliable ecological indicators to maximize translation into management frameworks that emphasize resilience-based state-and-transition models. Ecosystems must first be properly characterized with sound monitoring programs to facilitate the development of opportunistic management strategies that more accurately describes vegetation complexity of these plant communities. Further research should define triggers responsible for phase shifts of seeded communities and identify which factors other than fire, mechanical, or chemical treatment are responsible for ecosystem dynamics. Emphasis should also be given to characterize the influence of soils, climate, and grazing as interacting factors responsible for ecosystem change. As a tool for land managers, being able to characterize a site over time may help when planning for greater vegetation diversity and ecosystem functionality.

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Table 2-1. Principal components analysis loading matrix explaining axes variance for indicator species cover on 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>1.7</td>
<td>0.9</td>
</tr>
<tr>
<td>Percent</td>
<td>55.4</td>
<td>30.0</td>
</tr>
<tr>
<td>Cumulative percent</td>
<td>55.4</td>
<td>85.4</td>
</tr>
<tr>
<td>Variable</td>
<td>Eigenvectors</td>
<td></td>
</tr>
<tr>
<td>Crested wheatgrass</td>
<td>-0.67</td>
<td>0.17</td>
</tr>
<tr>
<td>Sandberg bluegrass</td>
<td>0.38</td>
<td>0.92</td>
</tr>
<tr>
<td>Wyoming big sagebrush</td>
<td>0.64</td>
<td>-0.37</td>
</tr>
</tbody>
</table>
Table 2-2. Mean (± 1 SE) species richness and diversity of the four community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means within a column followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Community phase</th>
<th>$n$</th>
<th>Species richness</th>
<th>Diversity ($H'$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>13</td>
<td>8.5 (0.6) b</td>
<td>0.88 (0.04) b</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>11.6 (0.8) a</td>
<td>1.15 (0.06) a</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>9.8 (0.7) ab</td>
<td>1.11 (0.05) a</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>9.1 (1.1) ab</td>
<td>0.98 (0.08) ab</td>
</tr>
</tbody>
</table>
Figure 2-1. Shaded-relief map of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass in the Northeastern Great Basin, USA.
Figure 2-2. Monthly precipitation (mm) collected from regional climate stations nearest to Wyoming big sagebrush communities historically seeded with crested wheatgrass.

Figure 2-3. Intensive Modified-Whittaker plot (Stohlgren et al. 1995) arrangement used for sampling vegetation cover and other variables of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass.
Figure 2-4. Plot of principal components analysis axes 1 and 2 for indicator species cover on 35 seeded Wyoming big sagebrush communities historically seeded with crested wheatgrass. Circles represent mean indicator species cover of respective communities delineated into community phases with hierarchical clustering.
Figure 2-5. Mean indicator species cover (± 1 SE) of the community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different \( (P < 0.05) \).
Figure 2-6. Mean herbaceous and shrub species cover (± 1 SE) of the community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different ($P < 0.05$).
Figure 2-7. Mean native and exotic herbaceous species cover (± 1 SE) of the community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different ($P < 0.05$).
Figure 2-8. State-and-transition model of Wyoming big sagebrush ecosystems emphasizing phases delineated for communities historically seeded with crested wheatgrass (Adapted from NRCS 2008a).
CHAPTER 3

INFLUENCE OF SOIL ATTRIBUTES ON VEGETATION OF WYOMING BIG SAGEBRUSH COMMUNITIES HISTORICALLY SEEDED WITH CRESTED WHEATGRASS

ABSTRACT

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is a dominant species on thousands of hectares of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities across the western United States. The influence of soil attributes and cultivation history on the vegetation of these seeded communities is not fully defined. I sought to characterize soil attributes of the four distinct community phases that exist within 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Community phases differed significantly for soil texture, soil nitrogen, and ground cover characteristics. Bare soil was almost double on loam-textured soils and rock cover was higher on clay loam texture soils ($P < 0.05$). Native plant cover was significantly higher on clay loam soils (7.2%) compared to loam soils (1.9%). Communities previously cropped had 6-fold lower native species cover, while exotic herbaceous and crested wheatgrass cover was double on sites that had been cropped. Percent sand was higher (28%) on communities with no cropping history compared to communities that had been cropped (16%), while higher silt percentages occurred on communities that had been previously cultivated. The reasons for choosing particular soils for cultivation are the same motives that influence vegetation differences between seeded communities. Cropping occurred on favorable, low rock, fine texture...
soils, the same soils that favor crested wheatgrass production and reduce resilience of
native plant composition. Characterizing soil attributes and disturbance history of seeded
Wyoming big sagebrush communities can provide information about feedback
mechanisms influencing dominant species that delineate community phases and the
organization of community structure.

**INTRODUCTION**

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is one of the most
commonly seeded exotic grass species in the western United States. Thousands of
hectares of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle
& Young) communities have been seeded since the 1930s throughout the Great Basin,
Snake River Plain, and the Columbia River Plateau (Young and Evans 1986). The largest
element of this practice was associated with the Halogeton Control Act of 1952, wherein
federal funding was granted to management agencies to plow large expanses of degraded
late-serial Wyoming big sagebrush communities in the eastern Great Basin and seed
crested wheatgrass to prevent the spread of the invasive species *Halogeton glomeratus*
(M. Bieb.) C.A. Mey. (Mathews 1986). Reclamation of abandoned dry-land farms and
unproductive sagebrush pastures on private and public land accounted for a large
majority of lands where crested wheatgrass was planted. Many of these seeded
communities have unique pre-seeding disturbance histories and soil attributes that may be
responsible for the composition of vegetation. However, much of this land continues to
be managed under the general assumption that seeded communities follow similar
successional trajectories. However, these communities assemble into four distinct phases
based on significant differences in crested wheatgrass and other dominant species cover (see Chapter 2). Understanding the mechanisms of soil-vegetation relationships in seeded Wyoming big sagebrush communities is needed to determine the factors responsible for the emergence of these community phases. Identifying key soil attributes and the potential influence of cultivation history on vegetation may help clarify the successional pathways portrayed in these seeded communities. With this knowledge, land managers can begin to understand the indicators and feedbacks responsible for some these distinct community phases and how to manage ecosystem resilience in sagebrush communities seeded with crested wheatgrass (Briske et al. 2008).

Dominant plant species productivity and structure in big sagebrush communities is determined by site specific soil properties, including texture, rock content, and elevation (Jensen et al. 1990). Moreover, cover of dominant bunchgrass species is strongly influenced by soil texture in big sagebrush communities (Davies et al. 2007). While it is clear that soils attributes and climate determine the structure and function of plant communities, dominant plant species may exert considerable control of community dynamics and alter soil attributes. For example, crested wheatgrass has been shown to negatively alter soil organic matter, phosphorus and nitrogen availability, and general soil quality in mixed-grass prairie ecosystems (Dormaar et al. 1995; Lesica and DeLuca 1996; Willms et al. 2005). However, Krzic et al. (2000) determined there was no degradation in soil properties when comparing native big sagebrush-steppe and seeded communities in the southern interior of British Columbia, Canada. Crested wheatgrass has also been considered a primary factor responsible for low plant diversity in mixed-grass prairie (Henderson and Naeth 2005) as well as sagebrush ecosystems (Marlette and Anderson
Given that four distinct community phases develop in sagebrush ecosystems seeded with crested wheatgrass, a pressing question remains as to whether these phases vary in soil attributes and historical disturbance regimes?

Disturbance regimes are defined on the basis of frequency, intensity, scale, and timing (Beever et al. 2003). The type of soil disturbance associated with rangeland seedings influence the structure of sagebrush-steppe communities (McLendon and Redente 1990). Soil attributes and soil disturbance history may help explain successional dynamics, the formation of distinct community phases, and assist with developing management strategies (Laycock 1991). Thus, my general objective was to characterize the influence of soil attributes and disturbance history on the vegetation of 35 Wyoming communities in the northeastern Great Basin that had been seeded with crested wheatgrass at least 30 or more years ago. Specifically, I compare community phases for these characteristics and clarify the potential role of these factors on determining successional trajectories. I anticipate this research will provide managers a greater understanding of how to develop resilience-based management models for crested wheatgrass seeded Wyoming big sagebrush communities.

**MATERIALS AND METHODS**

**Plant community selection and description**

Thirty-five Wyoming big sagebrush communities seeded with crested wheatgrass were selected for this study. Communities were located on public lands administered by Bureau of Land Management (BLM) field offices in Cassia and Oneida counties in Idaho,
Elko county Nevada, and Box Elder and Tooele counties in Utah (Figure 2-1).

Communities met the following criteria: 1) successful initial establishment of crested wheatgrass, 2) prescribed and natural fire have been not occurred since seeding, 3) chemical and or mechanical shrub removal treatments have not occurred since seeding, and 4) seedings were more than 30 years old. Each community was visited to validate criteria before inclusion in the study. Communities were primarily located in the northeastern Great Basin, a region central to seeding efforts associated with the Halogeton Control Act of 1952. Communities have a varied history of seeding treatment and soil disturbance history status since initial establishment including being cropped or not cropped prior to crested wheatgrass seeding (Table A-5). Cropping status and cultivation disturbance history describes pre-seeding soil disturbance from farming practices using plowing or disking in the production of dry-land grains, mainly located in the Onieda County, Idaho seeded communities.

Elevation of communities ranged from 1380-1788 meters above sea level with most occurring on similar terrain, typical of Great Basin Wyoming big sagebrush habitat (West 1988). Mean average annual precipitation (1972 to 2007) ranged from 178 to 382 mm and precipitation primarily occurs as winter snow and spring rain (WRCC 2008). Regional precipitation for the 2006-2007 growing season (1 October to 30 September) was approximately 50% of the 35-year average (Figure 2-2). All communities are currently, and have been, grazed by livestock since the late-1800s. Communities occurred on soils typical of Wyoming big sagebrush ecosystems with the majority being Aridisols and Mollisols, with some Entisols and Inceptisols (Table A-1).
**Sampling procedures**

Within each community, four 20 x 5 m plots were established at least 200 meters from fences, roads, water improvements, cultural resources, and landscape disturbances. Plots were also placed to avoid rock outcrops, bottom of washes, and steep slopes. Macro-topographic heterogeneity among plots was expected and could not be avoided. Plots were an intensive version of the Modified-Whittaker plot (Stohlgren et al. 1995), oriented by magnetic north-south bearings. Plots contained one 10 m$^2$ (5 x 2 m) and four 1 m$^2$ (2 x 0.5 m) subplots nested within the 100 m$^2$ plot (Figure 2-3). Plots were sampled during peak herbaceous productivity, corresponding to the period between May and June 2007. Percentage vegetation canopy cover for each plant species and ground cover category (bare ground, rock, litter, and crypto-biotic crust) were visually estimated within each 1-m$^2$ subplot following procedures of Stohlgren et al. (1995). Cover data was collected by one individual for all sites to minimize bias. Species richness was determined by totaling the number of different plant species present in 100-m$^2$ plots. Shannon-Weiner diversity ($H'$) was calculated from plant cover in 1 m$^2$ subplots using the following equation: \( H' = -\sum p_i \ln p_i \).

Four soil samples were collected at each Modified-Whittaker plot (Figure 2-3) by sampling a distance of 2 m diagonally away from each plot corner as to not disturb the vegetation of plots. The surface litter, if present, was removed and two 15-cm holes were dug within open spaces in the vegetation using a narrow trench shovel. From the side of both holes, a 5-cm wide vertical sliver to depth of hole was shaved, placed into a clean five-gallon bucket, mixed thoroughly and placed into quart-sized plastic bags for storage.
The 16 soil samples for each site were air-dried until further analyses. Data means were derived from averaging the four corners into one value for each plot.

Soils were analyzed for physical properties (particle size distribution and texture) and chemical properties (pH and total soil carbon and nitrogen). Particle size analysis or texture was determined using the standard hydrometer method (Gee and Bauder 1986). A 40.0 g-sample of air-dried soil from each plot was sifted through a < 2.0 mm sieve and mixed with 1 L of de-ionized water, shaken for 12 hours, and quantitatively analyzed using the standard method to determine percent sand, silt, and clay content of each sample. Soil pH was measured on a 15 g air-dried soil sample sieved through a 2.0 mm screen (Hendershot et. al. 1993). This sample was combined with 30 mL of de-ionized water (soil-water 1:2 w:v), stirred for 30 minutes, and allowed to settle for 1 h. Soil pH (to the nearest 0.1 pH unit) was determined using an Orion 3-Star bench-top pH meter and electrode (Thermo Scientific, Beverly, MA), immersed into the solution above the settled soil. Total soil N and C was determined for air-dried soil after passing through a 2.0 mm sieve, ground, and analyzed by direct combustion with a LECO CHN-2000 autoanalyzer (LECO Corp., St. Joseph, MI).

**Statistical analysis**

Ground cover and vegetation data were square root transformed to improve normality of many variables. Soil, cultivation history, and topography variables attained normality without being transformed, and appropriate outliers removed when necessary. Thus, all independent variables met the normality assumptions of analysis of variance (ANOVA). Analysis of variance (ANOVA) was used to analyze ground cover (bare
ground, litter, biological crust, and rock), soil physical properties (sand, silt, and clay), and soil chemical properties (carbon, nitrogen, and pH) for differences between the four community phases. Ground and vegetation cover variables, and species richness and diversity, of the 35 communities, were also compared for differences between soil texture classes (loam, silt loam, and clay loam) and disturbance history (cropped, non-cropped) using ANOVA. For significant ANOVA models, means were compared with Fisher’s LSD tests. All analyses were conducted with JMP 5.1 (SAS Institute, Cary, North Carolina, USA) using $P < 0.05$ to determine significance. Correlation between all variables, time since seeding, and community elevation was also performed with JMP 5.1.

RESULTS

Community phases

Sand content was higher and silt content was lowest in community phase 4 (Table 3-1). Total soil nitrogen in phases 2 and 3 exceeded the other two phases. There were no significant differences between phases in clay content and total soil carbon. Phase 3 had significantly lower soil pH than the other three phases. The most striking differences in ground cover between phases were for significantly higher bare soil and rock cover in phase 4 (Figure 3-1). Phase 4 also had lower biological crust cover than phase 2. Litter cover was not significantly different between the four community phases.
Soil texture classes and disturbance history

Four soil texture classes (loam, silt loam, and clay loam, and sandy loam) were found for the 35 communities. However, only the former two classes (n = 9, 23) were compared because only one community (Jackson) was classified as sandy loam, and two communities as clay loam (Bell Canyon and Brush Creek). Bare soil was 1.5-fold greater on communities with loam soils while biological crust cover was 1.7-fold greater on silt loam (Table 3-2). Native herbaceous plant cover and biological soil crust of silt loam soils were greater than loam soils. Of the dominant indicator species used to delineate community phases, Sandberg bluegrass cover was greater for silt loam than loam soils, whereas cover of crested wheatgrass and Wyoming big sagebrush was not significantly different between soil texture classes.

Cover of native herbaceous species, Sandberg bluegrass, and Wyoming big sagebrush was significantly greater on non-cropped than cropped communities (Table 3-3). Species richness and diversity were also significantly greater for non-cropped communities. In contrast, exotic herbaceous cover was 2-fold greater for cropped communities. Litter cover and percentage silt was significantly higher for cropped communities (Table 3-4), while percentage rock and sand was higher for non-cropped communities. Percentage clay and cover of bare soil and biological crust was not different between cropped and non-cropped communities.

Age of seeding and elevation

The number of years since communities were seeded (age) was positively correlated with biological crust cover ($n = 35, r = 0.40, P = 0.0193$), exotic species cover
(n = 33, r = 0.3464, P = 0.0457), and soil pH (n = 35, r = 0.31, P = 0.0678). In contrast, age of seeding was negatively correlated with rock cover (n = 32, r = -0.40, P = 0.0214) and species richness (n = 35, r = -0.30, P = 0.0868). Elevation was positively correlated with rock (n = 35, r = 0.374, P = 0.0248), sand (n = 34, r = 0.3742, P = 0.0325), and clay (n = 35, r = 0.374, P = 0.0275). Elevation was negatively correlated with litter (n = 33, r = -0.4796, P = 0.0048) and silt (n = 35, r = -0.412, P = 0.0133).

**DISCUSSION**

Complex interactions between soil, disturbance history, climate, and dominant plant species determine vegetation of ecosystems (West 1983). My results reveal that community phases differ for soil texture, total nitrogen, soil pH, and rock content. A key result shows vegetation as overwhelmingly dependent on soil attributes that existed prior to seeding with crested wheatgrass. These differences in soil attributes also appear to be a primary determinant of disturbance history of these communities because whether or not communities were cropped with dry-land grain production appears to depend on soil attributes, namely texture and rock content. Whether or not a plant community has the potential to reassemble with native species and big sagebrush is thus attributed to these general differences in soil attributes. A fundamental discovery of my study is that without an integrated assessment of soil attributes and disturbance history, vegetation differences of these communities could inaccurately be attributed to disturbances associated with cropping. Thus, below I explore how these interacting factors leave a lasting ecological legacy that explains a large degree of the variation in vegetation of these communities, even after an average of 48 years post-seeding with crested wheatgrass.
A common assumption is that crested wheatgrass forms mono-specific stands and is closed to reinvansion by native shrub species (Marlette and Anderson 1986; Henderson and Naeth 2005). This community phase does in fact exist, but the mechanisms underlying its formation need to be clarified. To begin, rock cover is a fundamental characteristic that determines the method chosen for seeding crested wheatgrass and whether a community is cropped. For example, communities where crested wheatgrass seed was broadcast had 2-fold greater rock cover. Not surprisingly, rock cover is positively correlated with elevation, indicative of alluvial and geological processes, providing lower elevation communities with more favorable cropping potential. Correlations also disclose that lower elevation soils have less sand and clay content, and higher silt content. Silt content was higher on cropped soils and sand was higher on non-cropped soils. Thus, fundamental differences in soil texture and surface topography dictated where and how crested wheatgrass was seeded. With this in mind, the role of these fundamental differences in soil can be linked to cover of the dominant indicator species used to delineate community phases (Chapter 2). Cropped soils with low rock and sand and high silt, are thus the primary factors responsible for significantly lower native species cover (herbaceous and big sagebrush), richness, and diversity of non-cropped soils. Quite the opposite, non-cropped soils with high sand and rock had nearly half the amount of exotic species cover, and one-third the amount of crested wheatgrass cover. Because soil texture, rock content, and elevation dictated whether a community was cropped, it is not possible to tease apart independence of these confounding factors. For example, the data I collected is unsuitable to determine whether the near absence of the native Sandberg bluegrass on cropped soils is a consequence of the disturbance history or
soil attributes of these communities prior to cropping and seeding crested wheatgrass. Even with this limitation, results of my study do not lend support to the notion that crested wheatgrass dominance, and the failure for successional phase shifts to higher diversity, is attributed to the competitive ability of crested wheatgrass.

Historical livestock grazing is generally associated with drastically altering Wyoming big sagebrush plant communities (Pickford 1932; Jones 2000). Because cattle primarily remove herbaceous vegetation, shrub cover typically increases under heavy grazing pressure (Frischknecht and Bleak 1957; Hull and Klomp 1966; Laycock and Conrad 1981; Whisenant 1990; Holechek et al. 1995). Heavy grazing has also been linked to the loss of biological crust cover in big sagebrush communities, even those seeded with crested wheatgrass (Memmott et al. 1998; Muscha and Hild 2006). Community phase 4 (Chapter 2) has characteristics that most closely resemble the vegetation responses of overgrazing: high shrub and bare ground cover with low herbaceous and biological crust cover. However, it is erroneous to imply that grazing alone was primarily responsible for the vegetation and ground cover characteristics of community phase 4. This shrub-dominated phase has significantly higher rock content, the highest sand content, and the lowest total soil nitrogen. These underlying differences in soil attributes provide evidence that conditions are more suitable to support shrub than herbaceous species, irrespective of grazing pressure, which was relatively consistent across the communities in this study (Table A-6). A more likely explanation is that grazing pressure facilitates the dominance of big sagebrush because soils more readily support shrubs than herbaceous species on communities delineated as phase 4. Soil texture differences in soil water-holding capacity and nutrient status are two possible
mechanisms that lend support to a soil-based explanation of the dominance of big sagebrush and low herbaceous species cover. Soil texture drives plant species assemblages based on the variation of water infiltration rates. For example, coarse soil texture is a common and consistent indicator of shrub dominance in big sagebrush communities (Jensen et al. 1990; Davies et al. 2007). Dominance of shrubs with coarse textured soils is possible because of reduced soil water-holding capacity and precipitation inputs that can more readily move through the topsoil and percolate to the subsoil and reach the deep-rooted shrubs (Dodd et al. 2002). Although, some shallow-rooted grass species may be benefiting through the dynamics of hydraulic redistribution of soil water from deep horizons to shallow horizons by big sagebrush (Ryel et al. 2004). Coarse textured soils also support less vegetation, especially of herbaceous species, than finer-textured soils (Davies et al. 2007). Low productivity and herbaceous species cover of coarse texture soils in sagebrush ecosystems is associated with lower soil nitrogen (Barker and McKell 1983; Jensen et al. 1990). Communities in phase 4 with coarse textured soils had nearly half the total nitrogen than the other three phases. Moreover, greater productivity of communities classified as silt loam is also supported by cover of biological soil crust, Sandberg bluegrass, and herbaceous species being significantly higher than communities with high bare ground cover and coarser loam soils. It is hard to overlook the importance of soil attributes when community phase 2 had the highest soil nitrogen, species diversity, cover of herbaceous species, biological crust, and the lowest bare soil.

My results support the generalization that succession in seeded communities is a convergent process controlled largely by existing soil attributes and their interactions.
with disturbance history (McLendon and Redente 1990). Not only am I incapable of evaluating these factors independently, it is difficult to ascertain the effects that cropping may have had on diminishing seed banks of native species. The available records also do not provide details of how many years communities were cropped. I suspect that in addition to the soil attributes, successional trajectories may also heavily depend on these undocumented effects on seed banks. Correlations between age of seeding and soil and vegetation attributes do however provide an indication of the importance of temporal dynamics in these communities. The negative correlation between rock cover and age of seeding is interesting because it suggests that low elevation communities with the best soils may have been the first to be seeded between 1950 and 1955, whereas the higher elevation sites were not seeded until the late 1960s. Reasons for this temporal pattern of seeding may be associated with rehabilitation efforts first focusing on damaged communities with the greatest potential that had been previously cropped before concentrating on the higher elevation rocky communities. Support for the assumption that communities first seeded may have been in poorer condition is obliquely based on older seedings having higher exotic species cover and lower species richness at the present (2007). While the communities first to be seeded may have been in the greatest need of repair, the positive correlation between age and biological crust cover provides an opportunity to speculate about how the difference in twenty years (i.e., 30 and 50 years since seeding) may have on the development of this important ecosystem component. My speculation is that this correlation is an artifact of biological crust cover being fundamentally low on upper elevation rocky sites and higher in the nitrogen rich finer-textured soils at lower elevations. Finally, lower pH of high elevation rocky sites may be
attributed to relict inputs from conifer leaf litter.

CONCLUSION

My results found that vegetation communities seeded with crested wheatgrass are a function of the interacting factors of soils and disturbance history. I sought to fill a gap in the understanding of these interactions and strengthen the ability to classify individual community phases in crested wheatgrass seeded Wyoming big sagebrush ecosystems. In the process of clarifying these relationships, it becomes obvious that the competitive effects of crested wheatgrass is likely not responsible for low diversity of community phase 1, and that heavy grazing is not responsible for dominance of big sagebrush in community phase 4. Instead, these results fit more closely with the ecological site concept currently in use by federal management agencies in the U.S. This central concept is based on the definition that ecosystems produce distinctive vegetation and respond to management depending on unique physical and soil attributes. In the future, management cannot overlook the limitations set by the ecological site, but must work within these limitations to provide ecologically-based active inputs to influence the underlying causes of plant succession (Pickett et al. 1987; Sheley et al. 1996; Krueger-Mangold et al. 2006).

LITERATURE CITED


Pyke, D. A. 1987. Demographic responses of *Bromus tectorum* and seedlings of
Agropyron spicatum to grazing by small mammals: the influence of demography and plant age. *Journal of Ecolology* 75: 825-835.


Table 3-1. Mean soil fractions, total soil carbon and nitrogen, and pH (± 1 SE) of the four community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means within a column followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Phase</th>
<th>n</th>
<th>Sand (± SE)</th>
<th>Silt (± SE)</th>
<th>Clay (± SE)</th>
<th>Carbon (± SE)</th>
<th>Nitrogen (± SE)</th>
<th>pH (± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13</td>
<td>28.2 (2.7) b</td>
<td>53.1 (2.8) a</td>
<td>18.6 (0.9)</td>
<td>1.840 (0.192)</td>
<td>0.042 (0.005) bc</td>
<td>8.32 (0.07) a</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>25.3 (3.6) b</td>
<td>56.4 (3.8) a</td>
<td>18.3 (1.3)</td>
<td>2.067 (0.261)</td>
<td>0.082 (0.008) a</td>
<td>8.23 (0.09) a</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>21.9 (2.9) b</td>
<td>58.6 (3.0) a</td>
<td>19.6 (1.1)</td>
<td>1.571 (0.208)</td>
<td>0.053 (0.007) b</td>
<td>7.43 (0.07) b</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>40.4 (4.8) a</td>
<td>40.1 (5.0) b</td>
<td>18.8 (1.8)</td>
<td>1.820 (0.345)</td>
<td>0.020 (0.011) c</td>
<td>8.47 (0.12) a</td>
</tr>
</tbody>
</table>
Table 3-2. Mean ground and vegetation cover (± 1 SE) for soil texture classes of 32 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means within a column followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Soil class</th>
<th>$n$</th>
<th>Bare soil</th>
<th>Biological crust</th>
<th>Native herbaceous</th>
<th>Sandberg bluegrass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loam</td>
<td>9</td>
<td>50.14 (0.09) a</td>
<td>5.21 (0.08) b</td>
<td>1.91 (0.11) b</td>
<td>0.60 (0.11) b</td>
</tr>
<tr>
<td>Silt loam</td>
<td>23</td>
<td>33.36 (0.04) b</td>
<td>9.01 (0.02) a</td>
<td>6.01 (0.04) a</td>
<td>4.34 (0.04) a</td>
</tr>
</tbody>
</table>
Table 3-3. Mean cover, species richness, and diversity (± 1 SE) of cropped and non-cropped Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means within a column followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Disturbance history</th>
<th>$n$</th>
<th>Native</th>
<th>Exotic</th>
<th>Crested wheatgrass</th>
<th>Sandberg bluegrass</th>
<th>Wyoming big sagebrush</th>
<th>Richness</th>
<th>Diversity ($H'$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cropped</td>
<td>5</td>
<td>0.78 (0.20) b</td>
<td>58.50 (0.36) a</td>
<td>28.03 (0.20) a</td>
<td>0.44 (0.22) b</td>
<td>1.42 (0.28) b</td>
<td>7.05 (0.99) b</td>
<td>0.779 (0.063) b</td>
</tr>
<tr>
<td>Non-cropped</td>
<td>30</td>
<td>5.18 (0.03) a</td>
<td>27.78 (0.06) b</td>
<td>12.22 (0.03) b</td>
<td>3.42 (0.4) a</td>
<td>8.00 (0.04) a</td>
<td>9.99 (0.41) a</td>
<td>1.074 (0.026) a</td>
</tr>
</tbody>
</table>
Table 3-4. Mean ground cover and soil fractions (± 1 SE) of cropped and non-cropped Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means within a column followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Disturbance history</th>
<th>n</th>
<th>Litter</th>
<th>Rock</th>
<th>Sand</th>
<th>Silt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cropped</td>
<td>5</td>
<td>16.28 (0.06) a</td>
<td>0.004 (0.209) b</td>
<td>16.89 (5.16) b</td>
<td>64.51 (4.63) a</td>
</tr>
<tr>
<td>Non-cropped</td>
<td>30</td>
<td>11.44 (0.01) b</td>
<td>2.903 (0.036) a</td>
<td>28.09 (1.88) a</td>
<td>53.90 (1.72) b</td>
</tr>
</tbody>
</table>
Figure 3-1. Mean ground cover (± 1 SE) of the community phases delineated for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
CHAPTER 4

CONCLUSION

Crested wheatgrass (Agropyron cristatum [L.] Gaertn.) is one of the predominant seeded species used in restoration or rehabilitation efforts on Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis) rangelands and plays an important role in our diverse western landscapes. Prior to this study, there was limited empirical information regarding the dynamic factors responsible for plant community phase identification and incorporation of resilience-based concepts in communities historically seeded with crested wheatgrass. This research characterized and expanded the view of community vegetation composition and explains some of the specific factors or mechanisms responsible for phase delineation in seeded Wyoming big sagebrush communities. The successional community phases within seeded Wyoming big sagebrush communities are more dynamic than previously described. Identifying successional mechanisms is necessary to understand community dynamics and anticipate future changes with management (Pickett et al. 1987). Moreover, identifying community phases is necessary to effectively evaluate, monitor, assess, and make resilience-based management decisions. With an accurate state-and-transition model, negative and positive feedbacks can be identified and managed.

In Chapter 2, I analyzed and characterized the important dominant species responsible for phase delineation between crested wheatgrass seeded communities. I also determined what vegetative factors were more likely to be significant contributors to these designations. I developed an expanded successional model highlighting the
differences between community phases. The most significant discovery of my results showed that in the absence of fire, herbicide, and mechanical treatments, four different phases emerge in historically seeded communities. Crested wheatgrass, Sandberg bluegrass (*Poa secunda* J. Presl), and Wyoming big sagebrush were important indicators that can be used for delineation of additional communities in the future. Phase 4 had the lowest herbaceous cover and highest shrub cover, and is considered the most at-risk to lose perennial cover if a major disturbance like wildfire were to occur. While many negative and positive feedbacks interact with each other to shape the composition of plant communities, the most important feedback is the one that can be identified and used in management-based decisions. Reducing the positive feedbacks that promote negative resilience in desirable phases of a seeded community can help direct or stabilize the direction of plant community succession toward a functional, stabilized weed resisting ecosystem (Sheley and Krueger-Mangold 2003). These results suggest that crested wheatgrass can occur in different phases of succession based on predisposed characteristics and resulting interactions, which influence the future plant community or state (Briske et al. 2008). Maintaining the desired phase in crested wheatgrass communities can be accomplished if the mechanisms influencing the pathways are characterized and understood by managers.

In Chapter 3, I characterized the interactions of successional community pathways in crested wheatgrass seeded communities. My efforts focused on variation in soil texture, soil pH, total nitrogen and carbon, and ground cover attributes. The study also attempted to identify the influence of soil class and cultivation history on seeded community characteristics. The most important conclusion is that pre-existing soil
attributes, cultivation history, and topographic characteristics are primarily responsible for influencing phase delineation in communities historically seeded with crested wheatgrass. Vegetation differences are not the result of crested wheatgrass competition, but of the mechanisms driving its dominance. The results for this study showed phase 4 was significantly different from phases 1-3 in having more coarse-textured soils. Additionally, bare-soil and rock cover was higher on phase 4 than phase 1. Furthermore, cropping status had significant effects on many vegetative, ground cover, and soil attributes. I concluded that pre-existing soil attributes and pre-seeding disturbance history have an important influence on current plant composition and succession in seeded communities (Elmore et al. 2006). Characterizing different interactions and feedback mechanisms of dominant species that delineate phases can provide a better account of community structure organization.

It has been suggested that crested wheatgrass is not diverse enough or that once a community has been seeded to crested wheatgrass it remains as a mono-specific community. However, my research found that seeded communities develop into multiple, weed-resistant communities, even while being grazed (West and Yorks 2002). Also, disturbance history and soil properties drive succession in crested wheatgrass ecosystems. While this study does not endorse crested wheatgrass as a cure-all solution to rangeland restoration in Wyoming big sagebrush communities, it is evident that crested wheatgrass, as a naturalized component on thousands of hectares of rangelands, can function as a desirable component of Wyoming big sagebrush communities. This study provides much-needed information for potential restoration and management of these important communities in the Great Basin.
LITERATURE CITED


APPENDICES
Table A-1. Soil classification characteristics: major component series, taxonomic classification, taxonomic order, and texture class for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass.

<table>
<thead>
<tr>
<th>Texture class</th>
<th>Taxonomic classification</th>
<th>Tax. order</th>
<th>Series</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bridge</td>
<td>Loamy-skeletal, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Darkbull</td>
</tr>
<tr>
<td>Cassia Creek</td>
<td>Loamy-skeletal, mixed, mesic Xerollic Durargids</td>
<td>Aridisols</td>
<td>Womack</td>
</tr>
<tr>
<td>Darby</td>
<td>Loamy-skeletal, mixed, mesic Xerollic Camborthids</td>
<td>Aridisols</td>
<td>Nibbs</td>
</tr>
<tr>
<td>HP&amp;P</td>
<td>Coarse-silty, mixed, mesic Xerollic Calcorthids</td>
<td>Aridisols</td>
<td>Bahem</td>
</tr>
<tr>
<td>Idahome</td>
<td>Coarse-silty, mixed, mesic Xerollic Calcorthids</td>
<td>Aridisols</td>
<td>Bahem</td>
</tr>
<tr>
<td>Jim Sage</td>
<td>Loamy-skeletal, mixed, mesic, shallow Xerollic Durorthids</td>
<td>Aridisols</td>
<td>Gunnell</td>
</tr>
<tr>
<td>Narrows</td>
<td>Loamy-skeletal, mixed, mesic Lithic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Saxby</td>
</tr>
<tr>
<td>Sandrock</td>
<td>Coarse-silty, mixed, mesic Calcixerollic Xerochrepts</td>
<td>Inceptisols</td>
<td>Heglar</td>
</tr>
<tr>
<td>Ward</td>
<td>Coarse-loamy, mixed, mesic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Escalante</td>
</tr>
<tr>
<td>Warm Creek</td>
<td>Loamy-skeletal, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Darkbull</td>
</tr>
<tr>
<td>Bowhuis</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>Cove</td>
<td>Fine-silty, mixed, mesic Calcic Haploxerolls</td>
<td>Mollisols</td>
<td>Kearns</td>
</tr>
<tr>
<td>East Black Pine</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>Grandine Bench</td>
<td>Coarse-loamy, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Ecur</td>
</tr>
<tr>
<td>Grandine Pond</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>Holbrook</td>
<td>Coarse-loamy, mixed, frigid Calcic Haploxerolls</td>
<td>Mollisols</td>
<td>Arbone</td>
</tr>
<tr>
<td>Roe</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>South Black Pine</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>Stone</td>
<td>Coarse-silty, mixed, mesic Sodic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Bayhook</td>
</tr>
<tr>
<td>Bell Canyon</td>
<td>Loamy-skeletal, mixed, mesic, shallow Xerollic Durorthids</td>
<td>Aridisols</td>
<td>Jericho</td>
</tr>
<tr>
<td>Brush Creek</td>
<td>Loamy, mixed, mesic, shallow Xerollic Durargids</td>
<td>Aridisols</td>
<td>Dewar</td>
</tr>
<tr>
<td>Jackson</td>
<td>Coarse-loamy, mixed, mesic Durixerollic Camborthids</td>
<td>Aridisols</td>
<td>Enko</td>
</tr>
<tr>
<td>Toano</td>
<td>Loamy-skeletal, mixed (calcareous), mesic Xeric Torriorthents</td>
<td>Entisols</td>
<td>Wiffo</td>
</tr>
<tr>
<td>Wilkins</td>
<td>Coarse-loamy, mixed, mesic Durorthidic Torriorthents</td>
<td>Entisols</td>
<td>Valmy</td>
</tr>
<tr>
<td>Buckskin</td>
<td>Loamy-skeletal, mixed, mesic Haploxerollic Durargids</td>
<td>Aridisols</td>
<td>Brobett</td>
</tr>
</tbody>
</table>
Table A-1 continued. Soil classification characteristics: major component series, taxonomic classification, taxonomic order, and texture class for 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass.

<table>
<thead>
<tr>
<th>Community</th>
<th>Texture class</th>
<th>Taxonomic classification</th>
<th>Tax. order</th>
<th>Series</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grouse Creek</td>
<td>silt loam</td>
<td>Coarse-loamy, mixed, superactive, mesic Xeric Argiurids</td>
<td>Aridisols</td>
<td>Lembos</td>
</tr>
<tr>
<td>Lynn</td>
<td>silt loam</td>
<td>Coarse-loamy, mixed, frigid Haploxerollic Durorthids</td>
<td>Aridisols</td>
<td>Rafriver</td>
</tr>
<tr>
<td>Red Butte</td>
<td>loam</td>
<td>Coarse-loamy, mixed, superactive, mesic Xeric Argiurids</td>
<td>Aridisols</td>
<td>Lembos</td>
</tr>
<tr>
<td>Yost</td>
<td>silt loam</td>
<td>Coarse-loamy, mixed, mesic Xerollic Calciorthids</td>
<td>Aridisols</td>
<td>Declo</td>
</tr>
<tr>
<td>Yost II</td>
<td>silt loam</td>
<td>Coarse-loamy, mixed, mesic Xerollic Calciorthids</td>
<td>Aridisols</td>
<td>Declo</td>
</tr>
<tr>
<td>Boulter</td>
<td>loam</td>
<td>Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Hiko Peak</td>
</tr>
<tr>
<td>Lofgren</td>
<td>loam</td>
<td>Fine-loamy, mixed, superactive, mesic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Taylorsflat</td>
</tr>
<tr>
<td>Lookout</td>
<td>loam</td>
<td>Loamy-skeletal, carbonatic, mesic, Petrocalcic Palexerolls</td>
<td>Mollisols</td>
<td>Bovvant</td>
</tr>
<tr>
<td>Onaqui</td>
<td>loam/silt loam</td>
<td>Fine-loamy, mixed, superactive, mesic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Taylorsflat</td>
</tr>
<tr>
<td>Russell</td>
<td>silt loam</td>
<td>Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids</td>
<td>Aridisols</td>
<td>Hiko Peak</td>
</tr>
</tbody>
</table>
Table A-2. Summary statistics for grass species cover of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agropyron cristatum</em></td>
<td>15.44 a</td>
<td>15.31</td>
<td>1.88</td>
<td>35.44</td>
<td>1.50</td>
</tr>
<tr>
<td><em>Poa secunda</em></td>
<td>4.07 b</td>
<td>2.75</td>
<td>0</td>
<td>15.88</td>
<td>0.69</td>
</tr>
<tr>
<td><em>Bromus tectorum</em></td>
<td>1.21 c</td>
<td>0.13</td>
<td>0</td>
<td>18.63</td>
<td>0.57</td>
</tr>
<tr>
<td><em>Elymus elymoides</em></td>
<td>0.19 c</td>
<td>0</td>
<td>0</td>
<td>3.19</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Pascopyron smithii</em></td>
<td>0.15 c</td>
<td>0</td>
<td>0</td>
<td>2.38</td>
<td>0.08</td>
</tr>
<tr>
<td><em>Pseudoroegneria spicata</em></td>
<td>0.13 c</td>
<td>0</td>
<td>0</td>
<td>3.56</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Poa bulbosa</em></td>
<td>0.10 c</td>
<td>0</td>
<td>0</td>
<td>3.31</td>
<td>0.09</td>
</tr>
<tr>
<td><em>Vulpia octoflora</em></td>
<td>0.08 c</td>
<td>0</td>
<td>0</td>
<td>1.25</td>
<td>0.04</td>
</tr>
<tr>
<td><em>Achnatherum hymenoides</em></td>
<td>0.05 c</td>
<td>0</td>
<td>0</td>
<td>0.50</td>
<td>0.02</td>
</tr>
<tr>
<td><em>Hesperostipa comata</em></td>
<td>0.04 c</td>
<td>0</td>
<td>0</td>
<td>1.00</td>
<td>0.03</td>
</tr>
<tr>
<td><em>Distichlis spicata</em></td>
<td>0.01 c</td>
<td>0</td>
<td>0</td>
<td>0.38</td>
<td>0.01</td>
</tr>
</tbody>
</table>

1Nomenclature follows NRCS 2008b.
Table A-3. Summary statistics for forb species cover of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ranunculus testiculatus</td>
<td>1.469 a</td>
<td>0.417</td>
<td>0</td>
<td>5.875</td>
<td>0.313</td>
</tr>
<tr>
<td>Phlox hoodii</td>
<td>0.218 b</td>
<td>0</td>
<td>0</td>
<td>2.500</td>
<td>0.091</td>
</tr>
<tr>
<td>Alyssum desertorum</td>
<td>0.150 bc</td>
<td>0</td>
<td>0</td>
<td>1.125</td>
<td>0.051</td>
</tr>
<tr>
<td>Collinsis parviflora</td>
<td>0.116 bc</td>
<td>0</td>
<td>0</td>
<td>1.000</td>
<td>0.044</td>
</tr>
<tr>
<td>Phlox longifolia</td>
<td>0.109 bc</td>
<td>0</td>
<td>0</td>
<td>2.250</td>
<td>0.066</td>
</tr>
<tr>
<td>Erigeron argentatus</td>
<td>0.077 bc</td>
<td>0</td>
<td>0</td>
<td>1.563</td>
<td>0.046</td>
</tr>
<tr>
<td>Lathyrus brachycalyx</td>
<td>0.063 bc</td>
<td>0</td>
<td>0</td>
<td>2.063</td>
<td>0.059</td>
</tr>
<tr>
<td>Opuntia polyacantha</td>
<td>0.050 bc</td>
<td>0</td>
<td>0</td>
<td>0.563</td>
<td>0.023</td>
</tr>
<tr>
<td>Astragalus lentiginosus</td>
<td>0.045 bc</td>
<td>0</td>
<td>0</td>
<td>1.190</td>
<td>0.034</td>
</tr>
<tr>
<td>Descurainia pinnata</td>
<td>0.032 c</td>
<td>0</td>
<td>0</td>
<td>0.188</td>
<td>0.009</td>
</tr>
<tr>
<td>Halogeton glomerata</td>
<td>0.023 c</td>
<td>0</td>
<td>0</td>
<td>0.313</td>
<td>0.012</td>
</tr>
<tr>
<td>Astragalus utahensis</td>
<td>0.023 c</td>
<td>0</td>
<td>0</td>
<td>0.417</td>
<td>0.013</td>
</tr>
<tr>
<td>Lipidium perfoliatum</td>
<td>0.021 c</td>
<td>0</td>
<td>0</td>
<td>0.375</td>
<td>0.012</td>
</tr>
<tr>
<td>Crepis acuminata</td>
<td>0.018 c</td>
<td>0</td>
<td>0</td>
<td>0.500</td>
<td>0.015</td>
</tr>
<tr>
<td>Sphaeralcea coccinea</td>
<td>0.018 c</td>
<td>0</td>
<td>0</td>
<td>0.250</td>
<td>0.009</td>
</tr>
<tr>
<td>Eriogonum microthecum</td>
<td>0.014 c</td>
<td>0</td>
<td>0</td>
<td>0.500</td>
<td>0.014</td>
</tr>
<tr>
<td>Hackelia micrantha</td>
<td>0.009 c</td>
<td>0</td>
<td>0</td>
<td>0.313</td>
<td>0.009</td>
</tr>
<tr>
<td>Lotus humistratus</td>
<td>0.007 c</td>
<td>0</td>
<td>0</td>
<td>0.188</td>
<td>0.006</td>
</tr>
<tr>
<td>Antennaria dimorpha</td>
<td>0.005 c</td>
<td>0</td>
<td>0</td>
<td>0.125</td>
<td>0.004</td>
</tr>
<tr>
<td>Epilobium halleanum</td>
<td>0.005 c</td>
<td>0</td>
<td>0</td>
<td>0.125</td>
<td>0.004</td>
</tr>
<tr>
<td>Eriogonum brevicaule</td>
<td>0.005 c</td>
<td>0</td>
<td>0</td>
<td>0.188</td>
<td>0.005</td>
</tr>
<tr>
<td>Allium acuminatum</td>
<td>0.004 c</td>
<td>0</td>
<td>0</td>
<td>0.125</td>
<td>0.004</td>
</tr>
<tr>
<td>Calochortus nuttallii</td>
<td>0.004 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Iva axillaries</td>
<td>0.004 c</td>
<td>0</td>
<td>0</td>
<td>0.125</td>
<td>0.004</td>
</tr>
<tr>
<td>Sisymbrium altissimum</td>
<td>0.004 c</td>
<td>0</td>
<td>0</td>
<td>0.125</td>
<td>0.004</td>
</tr>
<tr>
<td>Erodium cicutarium</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Ipomopsis aggregata</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Machaeranthera canescens</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Salsola kali</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Tragopogon dubius</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
<tr>
<td>Draba cuneifolia</td>
<td>0.002 c</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.002</td>
</tr>
</tbody>
</table>

1Nomenclature follows NRCS 2008b.
Table A-4. Summary statistics for shrub species cover of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different letters are significantly different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Artemisia tridentata spp.</em> wyomingensis</td>
<td>8.25 a</td>
<td>5.95</td>
<td>0.25</td>
<td>19.00</td>
<td>1.02</td>
</tr>
<tr>
<td><em>Artemisia nova</em></td>
<td>1.68 b</td>
<td>0</td>
<td>0</td>
<td>25.50</td>
<td>0.85</td>
</tr>
<tr>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td>0.82 bc</td>
<td>0.38</td>
<td>0</td>
<td>3.75</td>
<td>0.18</td>
</tr>
<tr>
<td><em>Ericameria nauseosus</em></td>
<td>0.33 c</td>
<td>0</td>
<td>0</td>
<td>7.00</td>
<td>0.20</td>
</tr>
<tr>
<td><em>Atriplex confertifolia</em></td>
<td>0.58 c</td>
<td>0</td>
<td>0</td>
<td>13.94</td>
<td>0.41</td>
</tr>
<tr>
<td><em>Gutierrezia sarothrae</em></td>
<td>0.14 c</td>
<td>0</td>
<td>0</td>
<td>1.88</td>
<td>0.07</td>
</tr>
<tr>
<td><em>Juniperus osteosperma</em></td>
<td>0.09 c</td>
<td>0</td>
<td>0</td>
<td>3.13</td>
<td>0.09</td>
</tr>
<tr>
<td><em>Artemisia spinescens</em></td>
<td>0.06 c</td>
<td>0</td>
<td>0</td>
<td>1.94</td>
<td>0.06</td>
</tr>
<tr>
<td><em>Sarcobatus vermiculatus</em></td>
<td>0.01 c</td>
<td>0</td>
<td>0</td>
<td>0.17</td>
<td>0.01</td>
</tr>
</tbody>
</table>

1 Nomenclature follows NRCS 2008b.
Table A-5. Characteristics of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass: age (years since seeding), year seeded, size of seeding (ha), disturbance history (cropped [C] and non-cropped [NC]), pre-treatment (plowed [P], herbicide [H], or chaining [C]), seeding method (broadcast [B], drill-seeded [D], or aerial-seeded [A]), and post treatment (harrowed [H] or none [N]).

<table>
<thead>
<tr>
<th>Site</th>
<th>Age</th>
<th>Year</th>
<th>Size</th>
<th>Disturbance history</th>
<th>Pre-treatment</th>
<th>Seeding method</th>
<th>Post treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bridge</td>
<td>52</td>
<td>1955</td>
<td>436</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Cassia Creek</td>
<td>38</td>
<td>1969</td>
<td>364</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Darby</td>
<td>40</td>
<td>1967</td>
<td>1012</td>
<td>NC</td>
<td></td>
<td></td>
<td>N</td>
</tr>
<tr>
<td>HP&amp;P</td>
<td>53</td>
<td>1954</td>
<td>845</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Idaho home</td>
<td>53</td>
<td>1954</td>
<td>554</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Jim Sage</td>
<td>40</td>
<td>1967</td>
<td>348</td>
<td>NC</td>
<td></td>
<td></td>
<td>N</td>
</tr>
<tr>
<td>Narrows</td>
<td>52</td>
<td>1955</td>
<td>630</td>
<td>NC</td>
<td>P</td>
<td>B</td>
<td>N</td>
</tr>
<tr>
<td>Sandrock</td>
<td>54</td>
<td>1953</td>
<td>969</td>
<td>NC</td>
<td>P</td>
<td>B</td>
<td>H</td>
</tr>
<tr>
<td>Ward</td>
<td>55</td>
<td>1952</td>
<td>324</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Warm Creek</td>
<td>57</td>
<td>1950</td>
<td>1755</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Bowhuis</td>
<td>34</td>
<td>1973</td>
<td>1955</td>
<td>C</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>Cove</td>
<td>42</td>
<td>1965</td>
<td>114</td>
<td>NC</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
<tr>
<td>E. Black Pine</td>
<td>55</td>
<td>1952</td>
<td>4149</td>
<td>C</td>
<td>P</td>
<td>D</td>
<td>N</td>
</tr>
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Table A-6. Mean (±1 SE) animal unit month (AUM) \((n = 1-31)\), allotment utilization \((n = 2-13)\), grazing system, season of use (spring [Sp], summer [S], fall [F], winter [W]) of 35 Wyoming big sagebrush communities historically seeded with crested wheatgrass.

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\(^1\)Data not available.