Seed Banks of Sagebrush Communities Seeded with Crested Wheatgrass

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SEED BANKS OF SAGEBRUSH COMMUNITIES SEEDED WITH CRESTED WHEATGRASS

by

Kevin L. Gunnell

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Range Science

Approved:

Christopher A. Call  Thomas A. Monaco
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UTAH STATE UNIVERSITY
Logan, Utah

2009
ABSTRACT

Seed Banks of Sagebrush Communities Seeded with Crested Wheatgrass

by

Kevin L. Gunnell, Master of Science
Utah State University, 2009

Major Professor: Christopher A. Call
Department: Wildland Resources

Crested wheatgrass (Agropyron cristatum [L.] Gaertn.) is one of the most commonly seeded exotic species in the western United States. Although many degraded Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) plant communities have been seeded with crested wheatgrass during rehabilitation efforts, seed banks of these communities have not been characterized. I sought to characterize and explain the variation among 33 seeded communities in the northeastern Great Basin. Hierarchical clustering and principal components analysis identified four possible seed bank categories in these communities. Seed bank categories varied from high to low crested wheatgrass dominance. The crested wheatgrass-dominated category is a particularly attractive setting to develop management strategies that reduce crested wheatgrass dominance and increase native plant diversity. It is also a common practice to seed crested wheatgrass in mixture with native species after a disturbance to increase diversity. Empirical estimates as to how the density of crested wheatgrass seed and seedlings interfere with native species establishment have not been defined. A greenhouse
experiment was established using an addition series design to determine the influence of interference between crested wheatgrass and four important native species. The existence of seed bank categories of Wyoming big sagebrush communities seeded with crested wheatgrass agrees with the hypothesis that seed banks closely resemble floristic composition. In addition, these results support the hypothesis that seed bank composition has a strong influence on succession in these communities, and characterizing seed banks is necessary to develop ecologically based management strategies for seeded Wyoming big sagebrush communities. Interference from crested wheatgrass on many native species suggests that further management practices to enhance diversity in crested wheatgrass-dominated communities are necessary to reduce competition from crested wheatgrass in the seed bank as well as the aboveground vegetation. These results also suggest that the practice of simultaneously seeding native species with crested wheatgrass may likely result in poor native species persistence unless combined seed bank density and seeding rate of crested wheatgrass is sufficiently low.

(99 pages)
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Kevin L. Gunnell
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CHAPTER 1
INTRODUCTION

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is an introduced perennial grass that has been seeded on thousands of hectares in the Great Basin, and represents one of the largest-scale land management manipulations within the region. In the 1950s, rangeland managers removed large expanses of big sagebrush (*Artemisia tridentata* Nutt.) and reseeded these areas with crested wheatgrass to improve forage potential and prevent the spread of weeds in this overgrazed region (Young et al. 1999). Since the 1970s, crested wheatgrass has been planted on public lands in the Great Basin, primarily following wildfires, for revegetation because of its competitive ability with invasive annual grasses like downy brome (*Bromus tectorum* L.). Hundreds of articles were published in scientific journals between 1950 and 1980, discussing the management implications of crested wheatgrass communities. The majority of these articles focused on methodologies to manage these communities for forage production while preventing sagebrush from reinvading. In our contemporary era of rangeland management, emphases have shifted to restoration of big sagebrush communities to improve species diversity, improve critical winter habitat for big game species, and protect habitat for threatened and endangered wildlife species.

Crested wheatgrass communities are a particularly attractive setting to improve Great Basin plant communities because these communities are characteristically more stable and less fire-prone than the large expanses of downy brome. While some studies have evaluated reseeding native species into crested wheatgrass-dominated communities
(Bakker et al. 1997; Bakker and Wilson 2001; Fansler 2007), studies on the ability of native species to naturally reestablish are lacking. In particular, little is known about seed bank diversity, seed bank persistence, and seed bank interference within crested wheatgrass communities. Filling this gap in knowledge may provide a mechanistic understanding of the factors limiting natural reinvansion by native species and help overcome the challenges associated with diversifying crested wheatgrass communities.

The objectives of my research are to characterize seed banks of numerous Wyoming big sagebrush communities in the northeastern Great Basin that have been historically seeded with crested wheatgrass. I also seek to examine how seed density influences interference between crested wheatgrass and four important native species (two grasses and two shrubs). From these studies, I elucidate how variation between seed banks in different communities and interference from crested wheatgrass may influence vegetation dynamics and succession of seeded communities. My research will help define potential successional thresholds and facilitate adaptive management of crested wheatgrass in the Great Basin. For example, if native species are adequately represented within seed banks, then successional management can focus on reducing competitive effects of crested wheatgrass on native species germination and emergence. Conversely, if native species are poorly represented within seed banks, then these seed-limited communities require seeding native species in addition to reducing the competitive effects of crested wheatgrass.
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 an 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 (Vale 1975; Rogers 1982); however, some locations may have been grass-dominated (Hull and Hull 1974). Variability in vegetation dominance in Great Basin sagebrush communities 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 forbs abundance has drastically declined (West 1988; Johnson 1989). Since large herbivores were not present in numbers to adversely impact herbaceous species, the decline in abundance has been attributed to poor grazing tolerance and the absence of intensive ungulate herbivory prior to European settlement (Mack and
Thompson 1982). Wildfires did occur, however, and because herbaceous species have the potential to readily regrow while sagebrush does not (Wright 1985), 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 invasive annual grasses replacing native herbaceous species (Young and Evans 1973; Monsen 1994). Foremost among these annual grasses are downy brome and medusahead (*Taeniatherum caput-medusae* (L.) Nevski), which produce high amounts of 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 ecosystems (Tourney 1894; Griffiths 1903; Pickford 1932). Consequently, land managers 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 (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

Identifying forage grasses to improve rangeland productivity was the research emphasis of early American range researchers such as P. B. Kennedy and A. W. Sampson at the turn of the 20th century (Chatterton and Young 2002). Many exotic grasses, including crested wheatgrass performed better than the available native species, and became the “gold standard” to use on former shrub-steppe and sagebrush rangelands (Young and McKenzie 1982). Crested wheatgrass was first introduced into the Northern Great Plains from Russia in 1898 and was 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 dry-land 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; Pellant 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.) by seeding crested wheatgrass throughout the Great Basin and beyond (Young and Evans 1986).
Establishing crested wheatgrass required modifying traditional agricultural techniques to fit a new set of obstacles associated with seedings on 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 diminished 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 success for establishment (Pellant et al. 2004; Pellant and Lysne 2005). Crested wheatgrass is still used in large-scale seedings on public land, but 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 persistent, naturalized component of plant communities 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, plentiful 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 reduces downy brome dominance better than native species because it germinates earlier and grows more rapidly at colder temperatures than many native species (Chatterton and Harrison 2003). Crested wheatgrass 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 (Springfield et al. 1967; Laycock and Conrad 1981; 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; Laycock and Conrad 1981; Sharp 1986; Caldwell et al. 1991; 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 reduces shrub seedling invasion more than native grasses (Blaisdell 1949;
Frischnecht and Bleak 1957; Schuman et al. 1982), without fire and subsequent management 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 establish 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 sagebrush 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). Over-utilization 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,
sagebrush is able to reinvade without periodic treatments to reduce sagebrush (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 seedings to be reinvaded by native sagebrush-steppe species from adjacent plant communities. Prescribed fire perpetuates crested wheatgrass dominance because it has a 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 reduce 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 2, 4-D and tebuthiuron successfully reduces 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).

Indirect, non-management factors may also influence successional trajectories in sagebrush 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 communities (Cook and Irwin 1992; West and Yorks 2006), but may also interact with management activities to determine vegetation status of seeded sagebrush communities (West 1988; Sharp et al. 1992). However, management activities that remove woody and herbaceous dicotyledonous species obscure the role that these indirect factors play in determining secondary succession within seeded communities because of the obvious impact shrub removal has had on maintaining crested wheatgrass dominance.

**Seed bank dynamics of communities seeded with crested wheatgrass**

Seed banks provide important insights into plant community dynamics including colonization and succession (Bazzaz 1979), population structure (Wilson 1992), and community structure (Yarranton and Morrison 1974). Seed banks are characterized spatially within the soil and litter, and temporally according to seed longevity (Williams et al. 1974; Reichman 1975; Young and Evans 1975; Freas and Kemp 1983; Kemp 1989; Simpson et al. 1989). Transient seed banks are viable for less than 1 year, while persistent
seed banks are viable longer than 1 year (Thompson and Grime 1979). In general, seed banks of annual species are more persistent than perennial species in arid and semiarid ecosystems (Noy-Meir 1973; Kemp 1989).

There is still little known about seed bank composition and its impact on succession within Wyoming big sagebrush communities seeded with crested wheatgrass over a broad representative area. As in other arid ecosystems (Henderson et al. 1988), studies have shown that the seed bank composition of sagebrush communities seeded with crested wheatgrass appear to closely resemble the current aboveground vegetation (Marlette and Anderson 1986; Pyke 1990; Ambrose and Wilson 2003; Henderson and Naeth 2005). The high seed productivity of crested wheatgrass (Pyke 1990) and the transient nature of the seed bank of many native species in these communities can create a negative feedback that perpetuates crested dominance in the seed bank. Crested wheatgrass may also be able to maintain dominance in the seed bank of these communities because of the lack of a seed source and the poor dispersal of native species (Marlette and Anderson 1986).

Negative feedbacks that maintain crested wheatgrass dominance in the seed bank can be minimized if initial kill of sagebrush and other shrubs is low (Johnson and Payne 1968; Marlette and Anderson 1986). Higher shrub populations create areas of increased seed capture (Nelson and Chew 1977; Guo et al. 1998), increased resource availability, and safe sites (Young and Evans 1975; Hassan and West 1986; Pugnaire and Lazaro 2000). Preferential use of crested wheatgrass over most shrub species by livestock creates an opportunity to use livestock to manipulate the seed banks of crested wheatgrass communities. Dominance of crested wheatgrass seed in the seed bank can be reduced by
repetitive heavy spring grazing since grazing directly impacts crested wheatgrass seed production and competition and creates opportunities for sagebrush to establish (Frischknecht and Bleak 1957; Hull and Klomp 1966; Harris et al. 1968; Rittenhouse and Sneva 1976).

Seed bank composition, or more specifically, seed density of species, may exert some control over successional trajectories of plant communities through its effects on interference between emerging seedlings (Sheley and Larson 1994; Francis and Pyke 1996; Velagala et al. 1997). Characterizing interference is often difficult because of complex interactions in biotic and abiotic factors. To address these issues, interference is often examined with artificial communities, under controlled greenhouse experiments (Gibson et al. 1999). Many statistical issues have been raised about some of the designs used to examine interference, primarily replacement series experiments (Jolliffe et al. 1984; Connolly 1986, 1997; Rejmanek et al. 1989; Roush et al. 1989; Firbank and Watkinson 1990; Snaydon 1991; Jolliffe 2000). A promising approach to overcome these issues has been the use of addition series experiments (Spitters 1983; Radosевич 1987). Studies using addition series mixed density designs have been used to compare interference of multiple species in many greenhouse studies (Prather and Callihan 1991; Sheley and Larson 1994; Velagala et al. 1997; Sheley and Half 2006; Young and Mangold 2008). The primary advantage of this design is its ability to describe both intraspecific and interspecific interference between species in a controlled system, and to show the amount of resource partitioning occurring between species. When crested wheatgrass dominates seed banks, it may have a disproportionate impact on seedling emergence of native species because of the well-recognized advantages for seedling

**Implications**

Diversifying crested wheatgrass communities is challenging because there is not a clear mechanistic understanding of the factors limiting natural reinvasion by native species. A cursory appraisal of numerous communities seeded with crested wheatgrass will yield examples where sagebrush has reinvaded as well as examples where low-diversity crested wheatgrass communities persist. My proposed research identifies seed bank characteristics of 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass (> 30 years old), where livestock grazing, initial seeding establishment success, soil properties, climate, and topography have variably shaped vegetation. These communities vary greatly in cover of sagebrush, crested wheatgrass, and native herbaceous species, and were recently delineated into four distinct successional phases (Williams 2009). Interpretation of seed bank composition focuses on contrasts between distinct categories formed from species abundances across a large spatial scale. In addition, I conducted a controlled greenhouse study to evaluate seedling growth interference between key native species and crested wheatgrass from seed banks constructed with variable seed densities. These studies help to determine whether seed limitation functions as a threshold to succession, and whether crested wheatgrass interference is proportionally greater than other native species. This research provides insights into management opportunities to satisfy contemporary and future rangeland management goals for sagebrush communities influenced by crested wheatgrass.
OBJECTIVES

After locating 33 Wyoming big sagebrush plant communities in the northeastern Great Basin that had been seeded with crested wheatgrass between 30 and 50 years ago, I evaluated species presence and abundance of seed banks. My objective was to determine whether communities can be categorized with hierarchical clustering and whether these potential seed bank categories differed for soil attributes and ground cover. My second objective was to evaluate the effects of seed bank density on interference between crested wheatgrass and four important native species (rubber rabbitbrush, *Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird; Wyoming big sagebrush, *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young; bluebunch wheatgrass, *Pseudoroegneria spicata* [Pursh] A. Löve; and bottlebrush squirreltail, *Elymus elymoides* [Raf.] Swezey ssp. *elymoides*) in replicated greenhouse experiments. Thus, this thesis not only provides a comprehensive assessment of seed banks across highly variable plant communities, but it also assesses the importance of vegetation and edaphic factors on seed bank composition. Finally, my controlled experiments provide an evaluation of the influence of crested wheatgrass seed bank density on early- and late-successional native grass and shrub species.

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Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is one of the most commonly seeded exotic species in the western United States, particularly in the Great Basin. Although many degraded Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plant communities have been seeded with crested wheatgrass during rehabilitation efforts, seed banks of these communities have not been characterized. I sought to characterize and explain the variation among 33 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. Seed banks were sampled adjacent to 20 x 5 m intensive Modified Whittaker plots that were used to measure species richness, diversity and cover of vegetation. Hierarchical clustering and principal components analysis of crested wheatgrass, all other grasses, and all forbs, identified four possible seed bank categories in these communities. Category 1 was dominated by crested wheatgrass (1633 seeds m⁻²) and had the lowest seed density of other grasses (82 seeds m⁻²). Categories 2, 3, and 4 had decreasing seed bank densities of crested wheatgrass and increasing seed bank densities of other species. Category 4 had the highest seed bank density of native species, though it also had the most seeds of the invasive annual grass
downy brome (*Bromus tectorum* L.) (390 m⁻²). The existence of seed bank categories agrees with the hypothesis that seed banks closely resemble floristic composition. In addition, these results support the hypothesis that seed bank composition has a strong influence on succession in these communities, and suggest that characterizing seed banks is necessary to develop ecologically based management strategies for seeded Wyoming big sagebrush communities.

**INTRODUCTION**

Seeding Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) to improve forage potential and control invasive plants (Young et al. 1999) represents one of the largest-scale land management manipulations within the Great Basin. 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). For many decades since the 1950s, seeded communities were actively managed with mechanical and chemical treatments to kill sagebrush and other undesired shrubs, and to 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 a community phase dominated by crested wheatgrass persists (Hull and Klomp 1966; West et al. 1979). In the absence of these influences, three additional community phases with greater species richness and sagebrush cover can
develop depending on soil attributes of communities (Williams 2009). Although multiple phases are possible for Wyoming big sagebrush communities seeded with crested wheatgrass, the potential for management activities to influence successional trajectories, including increasing big sagebrush cover and species diversity is uncertain (Pellant and Lysne 2005). This uncertainty is partially attributed to an insufficient characterization of seed bank composition of a broad array of communities that exist at distinct successional phases.

Although seed is produced aboveground, species existence in a community is perpetuated by seed storage, primarily within soil seed banks. Because most species within arid ecosystems rely entirely on seeds for dispersal and regeneration (Kemp 1989), seed banks are a source of community resilience after perturbations. Seed banks in arid ecosystems are often characterized by high spatial and temporal heterogeneity (Thompson 1987; Rundel and Gibson 1996). This heterogeneity in the distribution of seeds allows for the co-existence of many plant species (Thompson and Grime 1979; Reichman 1984). Seed abundance and composition in seed banks is dependent on input and dispersal, either directly from a source plant to soil, or by subsequent horizontal and vertical movements of the seed into or across the soil (Chambers and MacMahon 1994). Seed bank composition and abundance is also greatly influenced by the seed longevity of species in the soil. In arid ecosystems, annual species are generally classified as having a persistent seed bank that can survive for multiple years (Thompson and Grime 1979; Kemp 1989). Contrastingly, perennial species have a much more transient seed bank that typically doesn’t survive longer than one year (Thompson and Grime 1979; Kemp 1989). The abundance and composition of seed banks represent a primary source of new plant
material and may determine species composition (Luzuriaga et al. 2005) and ecosystem structure after perturbations (Eriksson and Ehrlen 1992). The driving mechanisms of seed bank composition and abundance can have substantial impact on the stability of a community and influence future successional trajectories of communities (Cabin and Marshall 2000; Cabin et al. 2000).

Some studies of seed banks have shown weak correlations between floristic and seed bank composition and abundance (Thompson and Grime 1979; Rabinowitz 1981; Roach 1983; Thompson 1986; Milberg 1995). This disparity may be due to residual carryover of persistent species in the seed bank from the pre-disturbance vegetation, variable dispersal mechanisms of species, and variable seed predation of species (Chambers and MacMahon 1994; Price and Joyner 1997; Luzuriaga et al. 2005). Pre-disturbance seed banks may play a large role in the composition of species that emerge and inhabit the seed bank shortly after disturbance (Luzuriaga et al. 2005; Nishihiro et al. 2006). However, the influence of pre-disturbance seed bank composition may be limited to a few years after the establishment of a seeding due to the transient nature of the native perennial species that tend to dominate the seed banks of Great Basin communities (Guo et al. 1999). Dispersal mechanisms of plants, such as those evolved to use wind and animals, may allow a species to build a presence in the seed bank of a community in which it is not currently present in the aboveground vegetation. Good dispersal of species from a distant seed source is a logical postulation for many species in this environment; however, Marlette and Anderson (1986) found that the presence of the species *Elymus elymoides* (Raf.) Swezey, which has good dispersal mechanisms, was limited in the seed bank and vegetation of crested wheatgrass-dominated sagebrush communities despite an
abundant seed source. Post-dispersal hazards influencing seeds, such as predation, may contribute extensively to any disparity between seed dispersed from aboveground vegetation and those that are active in the seed bank. High seed predation is a common occurrence in arid ecosystems (Hulme 1998). Often, large seed densities of species observed in the seed rain fail to become an active component of the seed bank due to predation, primarily by rodents (Price and Joyner 1997). Diversifying a community may be aided if the seed banks in low diversity crested wheatgrass-dominated big sagebrush communities show a large disparity from the aboveground vegetation and have maintained the presence of native species.

In contrast, studies indicate that seed bank composition in arid ecosystems may closely resemble the current floristic composition of the community (Henderson et al. 1988). This apparent correlation between aboveground vegetation and seed banks may be an effect of the transient nature of most native desert perennial species (Thompson and Grime 1979; Kemp 1989). Because these transient perennial species tend to dominate seed bank of arid communities (Gou et al. 1999), current vegetation may act as a consistent seed source recharging the seed bank and maintaining a species presence in the seed bank. Further disturbance may, therefore, limit later successional perennial species presence in the seed bank by limiting the seed sources (Henderson et al. 1988). Seed bank composition of sagebrush communities seeded with crested wheatgrass has similarly been shown to resemble the current aboveground vegetation (Marlette and Anderson 1986; Pyke 1990; Ambrose and Wilson 2003; Henderson and Naeth 2005). This can be greatly influenced by the presence of seed sources which can be facilitated though shrub re-establishment that increase native species presence in the seed bank and vegetative
composition (Marlette and Anderson 1986; Pugnaire and Lazaro 2000). When establishment of shrub species occurs, facilitative mechanisms such as seed safe sites, soil moisture, and propagule pressure from native species increase as the shrubs age (Young and Evans 1975; Hassan and West 1986; Pugnaire and Lazaro 2000). These mechanisms help to reduce the effect of the transient seed banks of most native species and increase correlation with vegetation.

Vegetation of sagebrush communities dominated by crested wheatgrass may contain a poor representation of native grasses and shrubs, and in turn these species are not represented in the seed bank. Wildfire and management treatments to limit shrub re-establishment reduce establishment of many native shrub species and have long-lasting effects on seeded Wyoming big sagebrush communities. This causes local extinction of fire-intolerant native species from the seed bank due to the loss of a seed source (Marlette and Anderson 1986; Pyke 1987; Anderson and Inouye 2001). However, many communities seeded with crested wheatgrass were spared these subsequent management treatments and have not experienced wildfire. This provides an ideal opportunity to evaluate how natural succession proceeds uninhibited by confounding factors across disparate landscapes. Furthermore, by evaluating seed banks in these communities, it is possible to clarify the processes responsible for the formation of community phases and the role of seed banks in community structure.

Further characterization of seed banks in Wyoming big sagebrush communities seeded with crested wheatgrass is critical to predict responses to disturbance and strategically determine appropriate management activities to influence successional trajectories. Seed bank composition may function as a quantitative indicator to more
accurately predict feedbacks and community resilience (Briske et al. 2008). My study characterizes seed banks of 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass (> 30 years old), where livestock grazing, initial seeding establishment success, soil properties, climate, and topography have variably shaped vegetation. Most importantly, I evaluated communities from all four successional phases that have been recently delineated for seeded Wyoming big sagebrush communities (Williams 2009), all of which have not experienced confounding wildfire or management treatments since their initial seeding. This approach may help clarify relationships between floristic and seed bank composition and assist with developing strategic management prescriptions for these important rangeland communities. If seed banks are deficient in native species, increasing their availability through seeding may be necessary; however, if seed banks are abundant with native species, then management techniques that modify site availability and species performance could be implemented (Krueger-Mangold et al. 2006).

MATERIALS AND METHODS

Community selection and criteria

Wyoming big sagebrush communities were selected from four Bureau of Land Management (BLM) districts (Table 2-1). Communities were selected based upon the following criteria: 1) successful initial establishment of crested wheatgrass seeding based on BLM records rating establishment as good or excellent, 2) prescribed and natural fire have been absent since seeding, 3) chemical and/or mechanical shrub removal treatments have not occurred since seeding, and 4) seeding had taken place more than 30 years ago.
Inclusion of only communities seeded more than 30 years ago allowed native species, primarily shrubs, to re-establish (Hull and Klomp 1966; Harniss and Murray 1973), and necessarily avoided communities seeded with a complex mixture of species (i.e., Russian wildrye, alfalfa, etc.), which became commonplace in the 1970s. Each potential community was visited to confirm criteria before inclusion in the study. Community selection also focused on the northeastern Great Basin because of its central location to seeding efforts associated with the Halogeton Control Act of 1952. A total of 33 communities met the criteria (Table 2-1; Fig. 2-1). Time since seeding ranged from 34-57 years, with an average of 48 years. Mature crested wheatgrass plants from each community were taxonomically characterized to determine identity of crested wheatgrass species planted at each site. Only one crested wheatgrass species was identified, *Agropyron cristatum* (L.) Gaertn.

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). Though other shrub species occurred in the communities (e.g., black sagebrush, *Artemisia nova* A. Nelson; shadscale saltbrush, *Atriplex confertifolia* [Torr. & Frém.] S. Watson; yellow rabbitbrush, *Chrysothamnus viscidiflorus* [Hook.] Nutt.; rubber rabbitbrush, *Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird; etc.), Wyoming big sagebrush was consistently the dominant shrub species. 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 (Fig. 2-2). All communities are currently, and have been, grazed
by livestock since the mid- to late-1800s. Five of the communities had been previously cropped before being seeded with crested wheatgrass. The majority of soils were classified as Aridisols and Mollisols, but there are some Entisols and Inceptisols.

Four Intensive Modified-Whittaker plots were established in each community to quantify species presence, cover, and diversity in spring of 2007. These plots contain one 10-m² and four 1-m² subplots nested within a 100-m² plot (20-m x 5-m) (Fig. 2-3). Only data from the 1-m² subplots was used for my study. From these data, four distinct successional phases were delineated (Williams 2009). Soil samples were also taken adjacent to each of the plots to determine the physical and chemical soil attributes of each site.

**Seed bank sampling and characterization**

Seed bank samples consisted of eight soil cores (2 cm diameter x 5 cm depth, including litter layer) taken from a 1-m² area outside and adjacent to each of the four Intensive Modified-Whittaker 1-m² subplots (Fig. 2-3) in October of 2007. The 16 samples from each community (4 samples plot⁻¹ x 4 plots community⁻¹) were placed at 5°C for three months to cold stratify seeds and help break dormancy. After stratification, soil samples were placed in germination flats (20 cm x 40 cm x 10 cm) filled with 5 cm of sand and partitioned into distinct 10 cm x 20 cm sections to accommodate the four samples from each plot. Samples were spread evenly over the surface of the sand and placed in a greenhouse with lights to give a 12 h. daylight period. Flats were organized in randomized blocks, watered with de-ionized water as needed to keep samples moist, and germinated seedlings were identified, counted, and removed weekly for two months to
determine seed bank composition and density. Unidentifiable seedlings were transplanted and grown to maturity for identification. After two-months, samples were air-dried and the above procedure was repeated. Due to the lack of germination in the second assessment, samples were only grown for one month.

**Statistical analysis**

Seed bank data were natural log (ln) transformed, after adding the lowest observed density to all communities to remove zeros, to improve normality of many species. However, normality could only be attained for crested wheatgrass: thus, species were combined according to their respective growth form (grasses excluding crested wheatgrass, forbs, and shrub) to create groups that met normality assumptions of analysis of variance (ANOVA). Because groups still did not meet assumptions of normality, only species that occurred in 5 or more communities were considered. Normality was not attained for individual species other than crested wheatgrass; however, they were met for combined other grasses (excluding crested wheatgrass) and combined forbs, but not shrubs. Species were further grouped by origin (native vs. exotic), and life form (perennial vs. annual) to create groups that met normality assumptions. The annual species group reached normality only after bur buttercup (*Ceratocephala testiculata* [Crantz] Roth) was removed. Crested wheatgrass, other grasses, and forbs were considered indicators, and were analyzed using Wards hierarchical clustering procedure, which grouped the 33 communities into distinct clusters, hereafter referred to as seed bank categories. Indicators 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 indicators to differences between communities.

Seed bank categories were compared for species groupings (indicators, origin and life form) using analysis of variance (ANOVA). Seed bank categories were also compared for vegetation and soil cover (crested wheatgrass, Sandberg bluegrass (*Poa secunda*), Wyoming big sagebrush, total native herbaceous, total exotic, bare soil, litter, rock, and biological crust), species richness, species diversity, soil variables (texture, percent sand, percent silt, percent clay, percent carbon, percent nitrogen, and pH), seeding method (drilled, broadcast, or aerial broadcast), seedbed preparation method (plowed, harrowed, or chained), post seeding treatment (none or harrowed), cropping history (cropped or non-cropped), age of seeding, and elevation collected for a companion study (Williams 2009). For significant ANOVA models, means were compared with Fisher’s LSD tests. The relationship between composition of seed banks and aboveground vegetation was determined with correlation analysis of seed bank density and vegetative cover of the three indicators. Descriptive statistics (mean, median, minimum, maximum, and standard error) were calculated for seed bank density of all species that occurred in the communities. Mean (± 1 SE) seed bank density for species that occurred in five or more communities is presented for seed bank categories, but was not analyzed because normality was not met for many species. All analyses, including hierarchical clustering, PCA, and ANOVA were conducted with JMP 5.1 (SAS Institute) using $P < 0.05$ to determine significance.
RESULTS

Indicators

Of the 49 plant species that emerged from samples for the 33 communities, 13 species were abundant (occurred in 5 or more communities) (Table A-1). To meet the assumptions of normality, the seed bank density of the abundant species were grouped into three indicators (i.e., crested wheatgrass, other grasses, and forbs). The seed density of these three indicators explained 77% of the variation of the first two PCA axes (Table 2-2). Axis 1 shows positive weightings for forbs and grasses other than crested wheatgrass, and a negative weighting for crested wheatgrass. In contrast, Axis 2 has positive weightings for all the grasses and a negative weighting for the forbs.

Seed bank categories

Hierarchic clustering of the three indicators identified four possible clusters, or seed bank categories, among the 33 communities (Fig. 2-4). The four seed bank categories also loosely clustered when communities were plotted using PCA axes 1 and 2 (Fig. 2-5). Crested wheatgrass seed density in category 1 was nearly twice that of all other grasses, but was not significantly higher than the forbs (Fig. 2-6). In contrast, crested wheatgrass seed density decreased significantly in categories 2 and 3, and category 4 was roughly half that of category 1. All other grasses did not significantly differ in seed density between categories 1, 2, and 3, but were nearly twice as high for category 4, which approximated the crested wheatgrass densities of category 1. Forbs seed densities had the highest density of any of the indicators. Forbs density was highest in categories 2 and 4, and lowest in categories 1 and 3. Forbs density explained most of
the difference between categories 2 and 3. Forbs also had high densities in the communities compared with the other indicators. The low density of forbs was not significantly different from the high densities of crested wheatgrass and all other grasses.

Exotic species seed density was significantly higher than native species seed density for all categories except for category 3 (Fig. 2-7). Category 3 also had a significantly lower density of exotic species than the other categories. Native species density closely followed the trend of other grasses, with category 4 being significantly greater than the other categories. The density of total exotic species was dependent on different individual species in each category, while total native species density primarily consisted of Sandberg bluegrass (*Poa secunda* J. Presl) (Table 2-3). Category 4 had the highest seed bank density of the invasive annual grass downy brome (*Bromus tectorum* L.) (Table 2-3). Perennial species seed density was higher than annual species seed density in all categories, but only significantly for categories 1 and 3 (Fig. 2-8). Seed density of annual species was similar for categories 1 and 3, and 2 and 4, respectively. Perennial species were highest in category 1, but were not significantly different from category 4. Categories 2 and 3 were nearly identical in perennial species seed density, but also were not significantly different from category 4.

The seed bank categories did not show significant differences among categories when compared using any of the soil variables, seeding methods, seedbed preparation methods, post seeding treatments, cropping history, age of seeding, or elevation determined by a companion study (Williams 2009) When categories were compared using soil cover percentages of communities, only the variables of rock and biological crust showed significant difference among categories. Category 3 had higher cover of
rock than the other three categories (Fig. 2-9). Cover of biological crust was lowest in category 1 and highest in category 4 (Fig. 2-9). When categories were compared using cover of vegetation the shrub species, Wyoming big sagebrush, was not significant among categories. Cover of native herbaceous species, Sandberg bluegrass, and crested wheatgrass was significantly different for seed bank categories 1 and 4 (Fig. 2-10). Cover of native herbaceous species and Sandberg bluegrass nearly mirrored each other, with the trend of increasing cover from categories 1 being the lowest to 4 being the highest. Oppositely, crested wheatgrass cover decreased significantly between categories 1 and 4.

Seed bank density of all three indicators was positively correlated with the aboveground cover of each indicator; crested wheatgrass ($n = 33$, $r = 0.57$, $P = 0.0005$); grasses other than crested wheatgrass ($n = 33$, $r = 0.79$, $P < 0.0001$); and forbs ($n = 33$, $r = 0.84$, $P < 0.0001$).

**DISCUSSION**

This study revealed that seed banks of sagebrush communities seeded with crested wheatgrass could be characterized into four categories based on seed bank composition of robust indicators. A common perception is that seeded communities maintain low diversity because crested wheatgrass effectively prevents the establishment of many native herbaceous plants (Bunting et al. 2003) and may actually impede re-establishment of species diversity in the community by maintaining dominance in the seed bank (Marlette and Anderson 1986; Anderson and Inouye 2001). This may be the case for those communities that fall into seed bank category 1. Dominance of crested wheatgrass in the seed bank of seeded communities can be maintained because of a lack...
of a seed source of native species and the poor dispersal of many of these species
(Marlette and Anderson 1986). Sagebrush seed are typically not dispersed more than a
few meters from the parent plant, and seed banks of this species are known to be transient
(Young and Evans 1989; Meyer 1994). Species that are able to disperse long distances,
such as rabbitbrush, and create a presence in the seed bank of seeded communities may
not be able to establish viable seedling and seed bank populations because of interference
from adult crested wheatgrass plants and the strong competition from crested wheatgrass
seedlings (Harris and Wilson 1970; Eissenstat and Caldwell 1988; Caldwell et al. 1991;
Bakker and Wilson 2001). The high seed productivity of crested wheatgrass (Pyke 1990)
and the transient nature and short persistence of many perennial species can create a
negative feedback that further limits establishment of native species in the seed bank.
Many of the perennial native species in these communities rely on vegetative growth and
attributes to survive periods of low resources and therefore typically have seed that is
short-lived and not persistent in the seed bank, or is transient (Thompson and Grime
1979; Kemp 1989). Surprisingly only 3 of the 33 communities were characterized as seed
bank category 1 (Table 2-1), typified by low species diversity and crested wheatgrass
dominance, to which these mechanisms would most strongly apply.

Results of this study provide a promising outlook for current emphases placed on
improving the structural diversity of Wyoming big sagebrush communities historically
seeded with crested wheatgrass because native species are increasingly present in seed
banks of categories 2-4. Sagebrush plants that re-establish following the initial seeding of
crested wheatgrass provide an abundant source of seed (Johnson and Payne 1968;
Marlette and Anderson 1986), and as sagebrush cover increases, areas of enhanced seed
capture are created (Nelson and Chew 1977; Guo et al. 1998) that provide favorable resource availability and safe sites for the establishment of other native species (Young and Evans 1975; Hassan and West 1986; Pugnaire and Lazaro 2000). An observed trend in these sagebrush communities is that cover of native species and biological crusts are positively correlated (Stohlgren et al. 2001; Hilty et al. 2004; Williams 2009). Similarly, my study shows that seed bank density of native species and biological crust cover are positively correlated. Biological crusts can increase resource availability (Eldridge 2000) as well as increase seed capture and safe sites (Boudell et al. 2002; Elmarsdottir et al. 2003). Communities that have seed bank categories 2 and 3 may therefore provide the best opportunities to develop management strategies to favor the emergence of the viable native seed bank combined with treatments to suppress the dominance of crested wheatgrass. Entirely different strategies should be developed for communities with seed banks in category 1. Some promise in diversifying category 1 may be achieved by decreasing the ecological resilience of communities (Briske et al. 2008) by capitalizing on the preferential use by livestock of crested wheatgrass over most shrub species and with repetitive heavy spring grazing that directly impacts crested wheatgrass seed production and creates opportunities for sagebrush to establish (Frischknecht and Bleak 1957; Hull and Klomp 1966; Harris et al. 1968; Rittenhouse and Sneva 1976).

While the correspondence between seed bank and floristic composition is a variable depending on a number of factors (Young and Evans 1975; Thompson and Grime 1979; Hassan and West 1986; Marlette and Anderson 1986; Kemp 1989; Pugnaire and Lazaro 2000; Anderson and Inouye 2001), my study adds a new dimension to this relationship because of the broad variability of communities evaluated. Previous seed
bank characterizations of sagebrush communities seeded with crested wheatgrass found that composition of seed banks and vegetation cover were positively correlated (Marlette and Anderson 1986; Pyke 1990; Ambrose and Wilson 2003; Henderson and Naeth 2005); however, each of these studies was conducted in communities that closely resemble seed bank category 1, i.e., vegetation dominated crested wheatgrass and low species diversity. An exciting aspect of my results is that this positive correlation also emerges for communities that vary widely in cover of crested wheatgrass (10.2 – 28.1%), and native herbaceous species (0.3 – 8.4%). While my results do not agree with those from ecosystems where a positive correlation was not observed (Thompson and Grime 1979; Rabinowitz 1981; Roach 1983; Thompson 1986; Milberg 1995), the reason for this disparity could be due to the transient nature of seed in these seeded communities caused by disturbance, high predation of seeds, and the short persistence of perennial species in the seed bank (Henderson et al. 1988; Henderson and Naeth 2005).

The current vegetation also appears to be the primary factor responsible for the differences in the four seed bank categories. While a number of environmental and management variables (i.e., soil variables, seeding method, community history, etc.) were unable to explain the variation among communities, vegetation cover was highly correlated with seed bank composition. This indicates that factors that influence the composition of the aboveground composition of species such as climate, grazing, fire, and chemical treatments, may also influence the composition of the seed bank in these communities.

Seed bank categories for Wyoming big sagebrush communities seeded with crested wheatgrass have not been previously identified or incorporated into current
management knowledge and practice. It is apparent that seed banks play a large roll in indicating and determining future successional trajectories of communities. Although, I did not seek to measure how seed banks influence 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). I am reluctant to suggest that seeded communities will ever resemble the potential natural (i.e., reference) community because crested wheatgrass and the native grasses that once inhabited the understory of Wyoming big sagebrush are so different in many functional attributes, including grazing tolerance, competitive ability, and response to soil disturbances. I do, however, suggest that communities with category 2 and 3 seed banks should be managed as naturalized systems in order to preserve the diversity that has established in them. After a disturbance such as fire, these communities would likely lose many of the native species that have established and become dominated by crested wheatgrass in both the vegetation and seed bank. Communities with category 4 seed banks (high density of native species and downy brome) should be managed with considerable care because they are likely the most susceptible category to annual grass invasion and conversion to an annual dominated community phase following a wildfire or other disturbance event.

**MANAGEMENT IMPLICATIONS**

Seed banks of Wyoming big sagebrush communities seeded with crested wheatgrass more than 30 years ago are variable among widely distributed locations in the northeastern Great Basin. This variation can be grouped into four seed bank categories.
Poor native species seed dispersal and negative feedbacks can maintain the dominance of crested wheatgrass in seeded communities (seed bank category 1). Dominance of crested wheatgrass may be diminished through early shrub re-establishment that can create positive feedbacks that allow for increased native establishment in the seed bank (seed bank categories 2-4) and aboveground composition. The current floristic composition and cover influence seed banks of seeded communities and appears to be a primary factor explaining differences among community seed banks and their composition. Management objectives to increase diversity in seeded communities should focus on communities with low seed bank diversity (category 1). Diversification efforts in these communities may be inhibited by density-dependent interference from crested wheatgrass seed dominance in the seed bank. Reducing the negative feedback caused by prolific seed production of crested wheatgrass through selective grazing or other management strategies may be a first step in increasing native species establishment. If diverse communities are the goal, seed bank categories 2 and 3 should be managed as naturalized ecosystems that maintain a diverse species composition. Much of this diversity would likely be lost after a fire or other disturbance event, with crested wheatgrass re-establishing and dominating the community both in the vegetation and seed bank. Care should be taken in managing communities that have category 4 seed banks. Though they show high amounts of native species in the seed bank, they also contain dangerously high downy brome densities (Hempy-Mayer and Pyke 2008). After a disturbance, this invasive annual could more easily dominate these communities than communities in seed bank categories 1-3.
LITERATURE CITED


Table 2-1. Characterization of crested wheatgrass study sites by State, managing Bureau of Land Management field office, county, year planted, and seed bank category.

<table>
<thead>
<tr>
<th>State</th>
<th>Field Office</th>
<th>County</th>
<th>Site Number</th>
<th>Site Name</th>
<th>Year Planted</th>
<th>Seed Bank Category</th>
</tr>
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<tbody>
<tr>
<td>Idaho</td>
<td>Burley</td>
<td>Cassia</td>
<td>1</td>
<td>Bridge</td>
<td>1955</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>Cassia Creek</td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>Darby</td>
<td>1967</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>Idahome</td>
<td>1954</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>Jim Sage</td>
<td>1967</td>
<td>3</td>
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<td></td>
<td></td>
<td>6</td>
<td>Narrows</td>
<td>1955</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>7</td>
<td>Sandrock</td>
<td>1953</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td>Ward Coop</td>
<td>1952</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>9</td>
<td>Warm Creek</td>
<td>1950</td>
<td>4</td>
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<tr>
<td>Idaho</td>
<td>Pocatello</td>
<td>Oneida</td>
<td>10</td>
<td>Bowhuis</td>
<td>1973</td>
<td>1</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>11</td>
<td>East Black Pine</td>
<td>1952</td>
<td>2</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>12</td>
<td>Grandine Bench</td>
<td>1962</td>
<td>4</td>
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<td></td>
<td></td>
<td></td>
<td>13</td>
<td>Grandine Pond</td>
<td>1962</td>
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<td></td>
<td></td>
<td></td>
<td>14</td>
<td>Holbrook</td>
<td>1969</td>
<td>4</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>15</td>
<td>Roe</td>
<td>1958</td>
<td>2</td>
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<tr>
<td></td>
<td></td>
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<td>16</td>
<td>South Black Pine</td>
<td>1953</td>
<td>1</td>
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<td></td>
<td></td>
<td>17</td>
<td>Stone</td>
<td>1954</td>
<td>2</td>
</tr>
<tr>
<td>Nevada</td>
<td>Elko</td>
<td>Elko</td>
<td>18</td>
<td>Bell Canyon</td>
<td>1953</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>19</td>
<td>Brush Creek</td>
<td>1952</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>20</td>
<td>Jackson</td>
<td>1970</td>
<td>3</td>
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<td></td>
<td></td>
<td></td>
<td>21</td>
<td>Toana Well</td>
<td>1965</td>
<td>3</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>22</td>
<td>Wilkins</td>
<td>1954</td>
<td>2</td>
</tr>
<tr>
<td>Utah</td>
<td>Salt Lake</td>
<td>Box Elder</td>
<td>23</td>
<td>Buckskin</td>
<td>1955</td>
<td>1</td>
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<tr>
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<td></td>
<td></td>
<td>24</td>
<td>Grouse Creek</td>
<td>1955</td>
<td>2</td>
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<td></td>
<td></td>
<td>25</td>
<td>Lynn</td>
<td>1957</td>
<td>2</td>
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<td></td>
<td></td>
<td>26</td>
<td>Red Butte</td>
<td>1967</td>
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<td></td>
<td></td>
<td></td>
<td>27</td>
<td>Yost I</td>
<td>1952</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>28</td>
<td>Yost II</td>
<td>1960</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>29</td>
<td>Boulter Pass</td>
<td>1954</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>Lookout Juniper</td>
<td>1964</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>31</td>
<td>Lofgren</td>
<td>1969</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>32</td>
<td>Onaqui</td>
<td>1969</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>33</td>
<td>Russell</td>
<td>1952</td>
<td>4</td>
</tr>
</tbody>
</table>
Table 2-2. Principal components analysis loading matrix explaining axes variance for indicator seed bank density on 33 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>Crested Wheatgrass</td>
<td>-0.57064</td>
<td>0.59795</td>
</tr>
<tr>
<td>Other Grasses</td>
<td>0.48639</td>
<td>0.79836</td>
</tr>
<tr>
<td>Forbs</td>
<td>0.66166</td>
<td>-0.07119</td>
</tr>
</tbody>
</table>
Table 2-3. Mean densities (seeds m\(^{-2}\)) of abundant species (present in at least 5 communities) for each of the delineated seed bank categories. Numbers in parentheses are the standard error.

<table>
<thead>
<tr>
<th>Species</th>
<th>3</th>
<th>12</th>
<th>11</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Category 1</td>
<td>Category 2</td>
<td>Category 3</td>
<td>Category 4</td>
</tr>
<tr>
<td><em>Agropyron cristatum</em></td>
<td>1633.33 (270.16)</td>
<td>272.92 (42.36)</td>
<td>225.76 (38)</td>
<td>65.48 (17.58)</td>
</tr>
<tr>
<td><em>Poa secunda</em></td>
<td>83.33 (60.09)</td>
<td>170.83 (87.57)</td>
<td>184.09 (95.54)</td>
<td>509.52 (169.33)</td>
</tr>
<tr>
<td><em>Descurainia sophia</em></td>
<td>66.67 (30.05)</td>
<td>127.08 (39.34)</td>
<td>78.03 (16.45)</td>
<td>25 (14.43)</td>
</tr>
<tr>
<td><em>Ceratocephala testiculata</em></td>
<td>66.67 (30.05)</td>
<td>4235.42 (1024.1)</td>
<td>88.64 (38.93)</td>
<td>3428.57 (1469.85)</td>
</tr>
<tr>
<td><em>Haloegeton glomerotus</em></td>
<td>33.33 (22.05)</td>
<td>16.67 (11.65)</td>
<td>18.94 (7.71)</td>
<td>3.57 (3.57)</td>
</tr>
<tr>
<td><em>Hackelia micrantha</em></td>
<td>16.67 (16.67)</td>
<td>35.42 (31)</td>
<td>20.45 (8.8)</td>
<td>3.57 (3.57)</td>
</tr>
<tr>
<td><em>Poa bulbosa</em></td>
<td>8.33 (8.33)</td>
<td>58.33 (22.68)</td>
<td>43.18 (18.49)</td>
<td>465.48 (321.66)</td>
</tr>
<tr>
<td><em>Alyssum desertorum</em></td>
<td>0 (0)</td>
<td>56.25 (32.15)</td>
<td>4.55 (4.55)</td>
<td>60.71 (48.75)</td>
</tr>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>0 (0)</td>
<td>75 (21.1)</td>
<td>25 (7.54)</td>
<td>64.29 (24.31)</td>
</tr>
<tr>
<td><em>Bromus tectorum</em></td>
<td>0 (0)</td>
<td>45.83 (43.61)</td>
<td>18.94 (9.67)</td>
<td>390.48 (227.7)</td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>0 (0)</td>
<td>68.75 (39.18)</td>
<td>0 (0)</td>
<td>92.86 (63.79)</td>
</tr>
<tr>
<td><em>Erigeron spp.</em></td>
<td>0 (0)</td>
<td>2.08 (2.08)</td>
<td>5.3 (3.6)</td>
<td>57.14 (53.09)</td>
</tr>
<tr>
<td><em>Microsteris gracilis</em></td>
<td>0 (0)</td>
<td>45.83 (26.26)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

\(^1\)Nomenclature follows NRCS 2008b.
Figure 2-1. Shaded-relief map of 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass in the Northeastern Great Basin, USA. See Table 2-1 for community names and information.
Figure 2-2. Graph of monthly precipitation (mm) featuring regional climate stations nearest to seeded Wyoming big sagebrush communities. Thick black line represents actual monthly precipitation totals for years 2005, 2006, and 2007. Thin black line represents 35-year monthly average for named climate station.
Figure 2-3. Intensive Modified-Whittaker plot (Stohlgren et al. 1995) arrangement used for sampling the seed bank, vegetation, and soils of 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass.
Figure 2-4. Dendrogram of Wards hierarchical cluster analysis of indicator seed density showing four possible seed bank categories. See Table 2-1 and Figure 2-1 for community names, information, and locations.
Figure 2-5. Plot of principal components analysis axes 1 and 2 for indicator seed density on 33 seeded Wyoming big sagebrush communities historically seeded with crested wheatgrass. Different symbols represent four different seed bank categories.
Figure 2-6. Natural log transformed mean indicator seed density (± 1 SE) of the seed bank categories delineated for 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
Figure 2-7. Natural log transformed mean of exotic and native species seed density (± 1 SE) of the seed bank categories delineated for 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
Figure 2-8. Natural log transformed mean of annual and perennial species seed density (± 1 SE) of the seed bank categories delineated for 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
Figure 2-9. Mean rock and biological crust ground cover (± 1 SE) of the seed bank categories delineated for 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
Figure 2-10. Mean cover of native herbaceous, Sandberg bluegrass, and crested wheatgrass species (± 1 SE) of the seed bank categories delineated for 33 Wyoming big sagebrush communities historically seeded with crested wheatgrass. Means followed by different lowercase letters are significantly different ($P < 0.05$).
CHAPTER 3

SEEDLING INTERFERENCE BETWEEN CRESTED WHEATGRASS AND EARLY- AND LATE-SUCCESSIONAL GREAT BASIN SPECIES

ABSTRACT

Wyoming big sagebrush communities (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) seeded with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) can maintain low plant diversity and crested wheatgrass dominance in certain successional phases. This crested wheatgrass-dominated phase is a particularly attractive setting to develop management strategies that reduce crested wheatgrass dominance and increase native plant diversity. Management strategies that only focus on reducing competition from adult plants of crested wheatgrass have failed to increase native establishment because of the dominance of crested wheatgrass in the seed bank. It is also a common practice to seed crested wheatgrass in mixture with native species after a disturbance to increase diversity. Empirical estimates as to how the density of crested wheatgrass seed and seedlings interfere with native species establishment have not been defined. A greenhouse experiment was established using an addition series design to determine the influence of interference between crested wheatgrass and four important native species (rubber rabbitbrush, *Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird; Wyoming big sagebrush; bluebunch wheatgrass, *Pseudoroegneria spicata* [Pursh] A. Löve; and bottlebrush squirreltail, *Elymus elymoides* [Raf.] Swezey ssp. *elymoides*). Crested wheatgrass strongly interfered with growth of both shrub species and bluebunch wheatgrass. Alternatively, the early-successional species, bottlebrush squirreltail, and
crested wheatgrass had similar effects on each other’s growth. Interference from crested wheatgrass on many native species suggests that further management practices to enhance diversity in crested wheatgrass-dominated communities are necessary to reduce competition from crested wheatgrass in the seed bank as well as the aboveground vegetation. These results also suggest that the practice of simultaneously seeding native species with crested wheatgrass may likely result in poor native species persistence unless combined seed bank density and seeding rate of crested wheatgrass is sufficiently low.

**INTRODUCTION**

Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities seeded with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) can develop low plant diversity when disturbance regimes and soil attributes are unfavorable for recruitment and survival of shrubs and broadleaf forbs (Mueggler and Blaisdell 1958; Klomp and Hull 1972; McLean and van Ryswyk 1973; Hull 1974; Evans and Young 1978; West 1988; Vallentine 1989; Cook and Irwin 1992; Sharp et al. 1992; Holechek et al. 1995; Krzic et al. 2000; West and Yorks 2006). Crested wheatgrass dominance provides resistance to invasive annual grasses like downy brome (*Bromus tectorum* L.) and an attractive setting to develop management strategies that reduce crested wheatgrass dominance followed by seeding with native shrubs, perennial grasses, and forbs to increase species diversity (Cox and Anderson 2004; Pellant and Lysne 2005). However, management efforts to reduce crested wheatgrass density and cover with mechanical (disking) and chemical (glyphosate) treatments in Wyoming big
sagebrush communities have had the opposite effect, and fail to increase the establishment of seeded species (Fansler 2007; Hulet et al. 2008). While these treatments effectively reduce and/or kill adult crested wheatgrass plants, young seedling density increases when released from competition (Ambrose and Wilson 2003). If treatments are to be effective in Wyoming big sagebrush communities seeded with crested wheatgrass, they must also reduce seed production of crested wheatgrass (Pyke 1990; Sharp et al. 1992), otherwise this exotic grass can dominate the seed bank (Marlette and Anderson 1986; Henderson and Naeth 2005). Establishment of native species can also be drastically reduced by crested wheatgrass when simultaneously seeded with crested wheatgrass (Waldron et al. 2005). The method of using crested wheatgrass with native species in a seed mixture has been encouraged by the Bureau of Land Management (BLM) since 1999 when the agency initiated the “Great Basin Restoration Initiative” to restore plant diversity and structure to communities in the Great Basin (Pellant et al. 2004; Pellant and Lysne 2005). However, empirical estimates of how the density of crested wheatgrass seed and seedlings interfere with common native species of Wyoming big sagebrush communities and often seeded with crested wheatgrass after a disturbance have not been defined.

In addition to dominating seed banks, seedlings of crested wheatgrass compete strongly with seedlings of native species (Eissenstat and Caldwell 1987; Jackson and Caldwell 1989). Crested wheatgrass is known to be a superior competitor to bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) and Wyoming big sagebrush (Caldwell et al. 1985, 1991). Furthermore, crested wheatgrass has consistently been
shown to have excellent seedling vigor when grown with native species (Eissenstat and Caldwell 1988; Caldwell et al. 1991; Bakker and Wilson 2001). The ability of crested wheatgrass to compete at the seedling stage is linked to its greater response to increased resources at the seedling stage (Jackson and Caldwell 1989; Huber-Sannwald et al. 1996) and its ability to germinate and grow under cold temperatures (Harris and Wilson 1970; Aguirre and Johnson 1991; Chatterton and Harrison 2003). These mechanisms of high competitive ability of crested wheatgrass are likely compounded when seed bank density of this exotic grass increase, which in turn may directly influence native species emergence and seedling productivity, and ultimately the successional potential within Wyoming big sagebrush communities seeded with crested wheatgrass following disturbances.

Early- and late-successional species may differ in their natural colonization potential in Wyoming big sagebrush communities dominated by crested wheatgrass because of differing seed dispersal abilities that increase their presence and abundance in the seed bank (Marlette and Anderson 1986; Chambers and MacMahon 1994). When seeded directly with crested wheatgrass, however, intraspecific and interspecific interference may influence the native species colonization potential through the recognized mechanisms of self-thinning or competition for limited resources (Pyke and Archer 1991). When applying management through mechanical and chemical treatments to reduce crested wheatgrass, the carryover of crested wheatgrass seed in the seed bank can still express a large amount of interference on native species seeded into the site (Fansler 2007). Seed and/or seedling density is a primary factor in determining the composition of the community that emerges after initiating seedbed preparation and
seeding native species into crested wheatgrass-dominated sites that have been treated to reduce competition from mature crested wheatgrass plants.

Characterizing interference between species is challenging because of the complexity of interacting biotic and abiotic factors in plant communities. To address these issues, interference is often examined with artificial communities under controlled greenhouse experiments (Gibson et al. 1999). Many statistical issues have been raised about some of the designs used to examine interference, e.g., primarily replacement series experiments (Jolliffe et al. 1984; Connolly 1986, 1997; Rejmanek et al. 1989; Roush et al. 1989; Firbank and Watkinson 1990; Snaydon 1991; Jolliffe 2000). Addition series designs overcome these issues (Spitters 1983; Radosevich 1987), and have been used in greenhouse experiments to describe interference between species (Prather and Callihan 1991; Sheley and Larson 1994; Velagala et al. 1997; Sheley and Half 2006; Young and Mangold 2008). The primary advantage of this design is the ability to describe both intraspecific and interspecific interference between species in a controlled system and to show the amount of resource partitioning occurring between species.

The objectives of this study were to examine how seed and seedling density influence interference between crested wheatgrass and early- and late-successional native shrub and grass species. Seed bank composition, or more specifically, seed density of species, may exert some control over successional trajectories of plant communities through its effects on interference between emerging seedlings (Sheley and Larson 1994; Francis and Pyke 1996; Velagala et al. 1997). When crested wheatgrass dominates seed banks or is seeded in mixture with native species after a disturbance, it may have disproportionate effects on seedling emergence of native species because of its well-
recognized advantages of seedling performance (Harris and Wilson 1970; Eisenstat and Caldwell 1988; Caldwell et al. 1991). This study evaluates whether crested wheatgrass interference is proportionally greater than native species with differing successional potentials and may provide insights into management opportunities to satisfy contemporary and future rangeland management goals for big sagebrush communities influenced by crested wheatgrass.

MATERIALS AND METHODS

Early- and late-successional native shrubs and grasses were sown with crested wheatgrass using an addition series design (Spitters 1983; Radosevich 1987) in replicated greenhouse experiments to evaluate seedling growth interference. The study was conducted in a greenhouse at the USDA Forage and Range Research Laboratory (FRRL) in Logan, Utah, during May and June 2008. The average daily temperature in the greenhouse during the study was 19.5°C. Rubber rabbitbrush (Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird ssp. consimilis (Greene) G.L. Nesom & Baird) seed was purchased from a commercial seed company (Granite Seed Company, Lehi, Utah) and Wyoming big sagebrush seed (Artemisia tridentata Nutt. ssp. wyomingensis Beetle & Young), collected from central Utah in 2007, was obtained from the Utah Division of Wildlife Resources (Great Basin Research Centre, Ephraim, Utah). Bluebunch wheatgrass (Pseudoroegneria spicata [Pursh] A. Löve; T-1753), bottlebrush squirreltail (Elymus elymoides [Raf.] Swezey ssp. elymoides; T-1735c), and crested wheatgrass, (Agropyron cristatum [L.] Gaertn. ssp. cristatum: CDII RI-05) seed was collected from Cassia county Idaho, Gooding county Idaho, and Cache county Utah respectively, in
2005, 2007, and 2005, respectively. Germination percentages were determined at 20°C for 14 days for all species in April 2008, and used to calculate seeding densities for experiments.

Plastic pots (11 cm diameter x 23.5 cm height) were filled with 2100 grams of a 3:1 sand and peat moss soil mix. Seeds were sown on the surface and covered with approximately 2 mm of soil. Soil moisture of pots was maintained at 25 % gravimetric soil water content with de-ionized water. The four native species were sown separately with crested wheatgrass in a four-way density matrix (Radosevich 1987) at the following 16 target densities: 100:100, 100:500, 100:1,000, 100:1,500, 500:100, 500:500, 500:1,000, 500:1,500, 1,000:100, 1,000:500, 1,000:1,000, 1,000:1,500, 1,500:100, 1,500:500, 1,500:1,000, 1,500:1,500 seeds m⁻². Density matrices were arranged in a randomized-complete-block design with 3 blocks (replications) in two 45-day trials. Trial 1 was conducted from May 6 through June 21, 2008, and Trial 2 was conducted from May 16 through July 1, 2008. Forty-five days after seeding, seedlings were counted, harvested at the soil surface, separated by species, and dried at 60°C for 48 hours to determine aboveground dry biomass.

Data were grouped by species then fit to multiple linear regression models described by Spitters (1983). The inverse of all species biomass per plant was predicted using the final densities per pot as independent variables. Models were:

\[ y_n^{-1} = \beta_{n0} + \beta_{nn}N_n + \beta_{nc}N_c \quad \text{(native species)} \]
\[ y_c^{-1} = \beta_{c0} + \beta_{cc}N_c + \beta_{cn}N_n \quad \text{(crested wheatgrass)} \]

where \( y_n \) and \( y_c \) represent the average aboveground biomass for native species and crested wheatgrass, respectively. \( N_n \) and \( N_c \) represent the density per pot of the native species and
crested wheatgrass, respectively. $\beta_{n0}$ and $\beta_{c0}$ represent the maximum aboveground biomass for native species and crested wheatgrass grown in isolation, respectively. A lower number indicates higher biomass due to the inverse operation. $\beta_{nn}$ and $\beta_{cc}$ quantify the intraspecific interference and $\beta_{nc}$ and $\beta_{cn}$ quantify the interspecific interference for the native species and crested wheatgrass models, respectively. The ratios ($\beta_{nn}: \beta_{nc}$ and $\beta_{cc}: \beta_{cn}$) determine the relative influence of each species on the variable response. For example, a ($\beta_{cc}: \beta_{cn}$) ratio of 2 indicates that crested wheatgrass influences itself twice as much as the native species. In other words, it would take two of the native species to equal the influence of one crested wheatgrass on the response variable.

The double ratio $[\beta_{nn}/\beta_{nc}: \beta_{cc}/\beta_{cn}]$ was used to determine niche differentiation between species (Spitters 1983). Niche differentiation increases as the ratio departs from unity (1.0), meaning that native species and crested wheatgrass growth are decreasingly limited by the same resource. Non-significant competition coefficients indicate complete niche differentiation with no interaction between species.

Scatterplots of the residuals vs. predicted values were used to determine the homogeneity of variances and the degree of model fit. Significance of regression coefficients was determined with $P < 0.05$.

RESULTS

Germination of sagebrush and rabbitbrush was higher than predicted from preliminary germination percentage tests. Actual densities ranged from 300 – 15000 seedlings m$^{-2}$ for sagebrush and from 100 – 3000 seedlings m$^{-2}$ for rabbitbrush. However, these densities still provided a testable density matrix. Models were initially run with trial
as a main effect, but Trial 1 and Trial 2 showed significant ($P < 0.01$) differences for all species, except sagebrush, and were therefore modeled separately. The main difference between trials was significantly higher biomass for all species, except sagebrush, in Trial 2.

For both shrub species, interspecific interference was much more important than intraspecific interference for predicting biomass and vice versa for crested wheatgrass when grown with shrubs (Tables 3-1 and 3-2). Sagebrush had only a tenth of the influence of crested wheatgrass on its own biomass (Table 3-1), while crested wheatgrass had approximately 23-times the influence on its own biomass (Table 3-2). Rabbitbrush biomass reflected similar patterns of influence as sagebrush, although the influence of interspecific interference was lower (Tables 3-1 and 3-2).

The model predicting bluebunch wheatgrass biomass was not influenced by either intraspecific or interspecific interference in Trial 1, but was more influenced by interspecific interference in Trial 2 (Table 3-1). Crested wheatgrass biomass was influenced more by intraspecific interference in both Trials (Table 3-2). There was little to no difference between the influence of intraspecific and interspecific interference in predicting the biomass of bottlebrush squirreltail. There was no difference in Trial 1 between the influence of intraspecific and interspecific interference, though bottlebrush squirreltail appears to be influenced slightly more by intraspecific interference in Trial 2 (Table 3-1 and 3-2).

The double ratio $[\beta_{nn}/\beta_{nc}: \beta_{cc}/\beta_{cn}]$ analysis showed that resource partitioning occurred between crested wheatgrass and both shrub species, and crested wheatgrass and bluebunch wheatgrass. Of all native species, rabbitbrush showed the highest degree of
resource partitioning with crested wheatgrass. Bottlebrush squirreltail showed little to no resource partitioning with crested wheatgrass (Table 3-3).

**DISCUSSION**

Interference from highly competitive crested wheatgrass plants and seedlings is a possible mechanism that perpetuates low diversity in certain community phases of Wyoming big sagebrush communities (Marlette and Anderson 1986; Henderson and Naeth 2005; Fansler 2007). Crested wheatgrass proved to be highly competitive with these native species, i.e., crested wheatgrass biomass was influenced more by intraspecific interference and the native species were influenced more by interspecific interference. Species that are more influenced by intraspecific than interspecific interference are considered more competitive (Aarssen 1983; Pyke and Archer 1991), which corroborates with the previously identified growth characteristics of crested wheatgrass. As the density of crested wheatgrass increases, competition for resources during seedling establishment increases for these native species. Highly competitive species can increase time to reproductive maturity, decrease growth rates and viable seed production, or increase susceptibility to density-dependent and density-independent mortality of subordinate species (Pyke and Archer 1991). However, not all native species were negatively impacted by crested wheatgrass interference. Bottlebrush squirreltail proved to be either equally or more competitive than crested wheatgrass at the seedling stage. For the other species, crested wheatgrass interference negatively affected seedling growth, which suggests that establishment and growth of these native species may be hindered by crested wheatgrass under certain conditions.
Successional potential of species may determine a species’ ability to compete and establish in low diversity sagebrush communities dominated by crested wheatgrass. Early-successional species have attributes that give them advantages for natural re-establishment, including long-range seed dispersal mechanisms, nutrient use efficiency, and competitive growth rates and growth strategies (Huston and Smith 1987). However, some of these advantages may be lost when species are seeded on rangelands. For example, rabbitbrush and bottlebrush squirreltail have good dispersal mechanisms that allow them to exert propagule pressure far from the parent plant (Jones 1998; Meyer and Carlson 2001). When seeded directly with other native species that do not have these mechanisms, advantages for natural re-establishment are lost. Still, other attributes may offer them an advantage in establishment. My study showed that rubber rabbitbrush has higher resource partitioning at the seedling stage than sagebrush when grown with crested wheatgrass. This may help to decrease interspecific interference from crested wheatgrass (Sheley and Larson 1994) and allow for advantages in later growth over sagebrush when grown with crested wheatgrass. The high partitioning of resources of both shrub species from crested wheatgrass likely comes from differential uptake of soil and water resources (Frischknecht 1963; Cline et al. 1977; Matzner and Richards 1996; Donovan et al. 1999; Leffler et al. 2004), and root growth and form (Frischknecht 1963; Jackson and Caldwell 1989; Bilbrough and Caldwell 1997).

Not surprisingly, the grasses differed from shrubs in this study. The early-successional species, bottlebrush squirreltail, was influenced less by interspecific interference from crested wheatgrass than the late-successional species, bluebunch wheatgrass. In contrast to bluebunch wheatgrass, bottlebrush squirreltail also
demonstrated little to no resource partitioning with crested wheatgrass. These results suggest that it is not resource partitioning, but accelerated growth-rates and ability for resource acquisition that increases the influence of intraspecific interference on bottlebrush squirreltail’s biomass when grown with crested wheatgrass (Jones 1998). Thus, early-successional species may maintain some advantage in establishment even when seeded on rangelands.

Differences in density-dependent interference and resource partitioning make some species more suitable than others for diversifying low-diversity sagebrush communities dominated by crested wheatgrass. How these species are influenced by interference should also dictate the management treatments used to reduce crested wheatgrass competition in rangeland seedings. Treatments commonly focus on reducing competition from adult crested wheatgrass plants (Bakker et al. 1997; Fansler 2007; Hulet et al. 2008), but may leave a well-established seed bank of crested wheatgrass seed (Marlette and Anderson 1986; Henderson and Naeth 2005). Fansler (2007) found that mechanical and chemical treatments of adult plants facilitated the emergence of crested wheatgrass from the seed bank. Reducing competition from adult plants may be sufficient for species that are influenced minimally by interference from crested wheatgrass seedlings, such as bottlebrush squirreltail, but not for those that are significantly influenced by interference from crested wheatgrass, such as Wyoming big sagebrush and rubber rabbitbrush and to a lesser extent bluebunch wheatgrass. If establishment of a more diverse mixture of species is desired, treatments to reduce the seed banks of crested wheatgrass should also be developed and used. Possible treatments may include high intensity grazing or chemical treatments at critical developmental stages to reduce crested wheatgrass competition.
wheatgrass seed production over multiple years. Because of the intense influence of interference, even at low densities, my results suggest that the practice of seeding native species and crested wheatgrass together may compromise the establishment of many desirable native species as has been observed in rangeland seedings (Waldron et al. 2005).

**MANAGEMENT IMPLICATIONS**

This study has important implications for low-diversity, crested wheatgrass-dominated communities seeded with native species (Cox and Anderson 2004), and for rangeland seedings where crested wheatgrass is seeded with a mixture of native species following severe disturbances (Pellant et al. 2004; Pellant and Lysne 2005). Crested wheatgrass is considered a highly competitive species (Harris and Wilson 1970; Eissenstat and Caldwell 1988; Caldwell et al. 1991), and my study emphasizes that it interferes with the growth of several important native species at the seedling stage, and may likely limit their establishment in rangeland settings. Early-successional species, such as bottlebrush squirreltail, appear to be less impacted by crested wheatgrass interference at the seedling stage than later-successional species. This may be due to differences in resource partitioning or in species ability for early season growth and resource acquisition. My results suggest that interference from crested wheatgrass seedlings emerging from the seed bank should be anticipated and treatments to reduce seed production need to be applied prior to conducting rangeland seedings to promote species diversity. Similarly, significant crested wheatgrass interference on seedlings of the two shrub species and bluebunch wheatgrass provides strong evidence that the practice of simultaneously
seeding native species with crested wheatgrass may reduce establishment of seeded species, even at low crested wheatgrass seeding density.

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50:523-529.


The table 3-1. Multiple regression coefficients from the prediction equation ($y_n^{-1} = \beta_{n0} + \beta_{nn}N_n + \beta_{nc}N_c$)\(^1\) of native species seeded with crested wheatgrass aboveground biomass (g) and native seedling density.

<table>
<thead>
<tr>
<th>Native Species</th>
<th>Individual Seedling $\beta_{n0}$</th>
<th>Intraspecific Interference $\beta_{nn}$</th>
<th>Interspecific Interference $\beta_{nc}$</th>
<th>Interference Ratio $\beta_{nn}/\beta_{nc}$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARTR(^2)</td>
<td>138.1340</td>
<td>0.0215</td>
<td>0.2247</td>
<td>0.0957</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>(28.1176)(^3)</td>
<td>(0.0026)</td>
<td>(0.0240)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ERNA T1</td>
<td>83.7271</td>
<td>0.0174</td>
<td>0.0762</td>
<td>0.2279</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>(14.1262)</td>
<td>(0.0074)</td>
<td>(0.0121)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ERNA T2</td>
<td>67.6873</td>
<td>0.0206</td>
<td>0.0555</td>
<td>0.3700</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>(12.9997)</td>
<td>(0.0061)</td>
<td>(0.0108)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEL T1</td>
<td>5.8405</td>
<td>0.0087</td>
<td>0.0086</td>
<td>1.0128</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>(0.9107)</td>
<td>(0.0007)</td>
<td>(0.0008)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEL T2</td>
<td>5.6469</td>
<td>0.0123</td>
<td>0.0080</td>
<td>1.5376</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>(1.0818)</td>
<td>(0.0009)</td>
<td>(0.0009)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PSSP T1</td>
<td>7.1735</td>
<td>0.0148</td>
<td>0.0151</td>
<td>0.9777</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>(2.3124)</td>
<td>(0.0018)</td>
<td>(0.0019)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PSSP T2</td>
<td>8.8599</td>
<td>0.0140</td>
<td>0.0204</td>
<td>0.6845</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>(2.7871)</td>
<td>(0.0024)</td>
<td>(0.0024)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) $\beta_{n0}$, inverse mean biomass of and individual plant of the seeded native species grown in isolation; $\beta_{nn}$, intraspecific interference of seeded native species; $\beta_{nc}$, interspecific interference with crested wheatgrass; $\beta_{nn}/\beta_{nc}$, relative interference ratio of the seeded native species and crested wheatgrass; $R^2$, coefficient of determination.

\(^2\) ARTR = sagebrush, ERNA = rabbitbrush, ELEL = squirreltail, and PSSP = bluebunch wheatgrass. T1 and T2 designate Trial 1 and Trial 2, respectively.

\(^3\) Standard errors for coefficients significantly different from zero (P < 0.05).
Table 3-2. Multiple regression coefficients from the prediction equation \(y_c^{-1} = \beta_c0 + \beta_{cc}N_c + \beta_{cn}N_n\)\(^1\) of crested wheatgrass seeded with native species aboveground biomass (g) and crested wheatgrass seedling density.

<table>
<thead>
<tr>
<th>Native Species</th>
<th>Individual Seedling</th>
<th>Intraspecific Interference</th>
<th>Interspecific Interference</th>
<th>Interference Ratio</th>
<th>R(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARTR T1(^2)</td>
<td>6.2902</td>
<td>0.0099</td>
<td>0.0004</td>
<td>23.6219</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>(1.9524)(^3)</td>
<td>(0.0016)</td>
<td>(0.0002)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ARTR T2</td>
<td>4.0036</td>
<td>0.0144</td>
<td>0.0006</td>
<td>22.8978</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td>(1.7858)</td>
<td>(0.0015)</td>
<td>(0.0002)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ERNA T1</td>
<td>2.8438</td>
<td>0.0112</td>
<td>0.0006</td>
<td>17.7925</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>(0.8548)</td>
<td>(0.0007)</td>
<td>(0.0004)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ERNA T2</td>
<td>6.6762</td>
<td>0.0122</td>
<td>0.0003</td>
<td>43.2253</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>(1.0274)</td>
<td>(0.0009)</td>
<td>(0.0005)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEL T1</td>
<td>3.0556</td>
<td>0.0093</td>
<td>0.0093</td>
<td>1.0021</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>(1.3593)</td>
<td>(0.0012)</td>
<td>(0.0011)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEL T2</td>
<td>5.4591</td>
<td>0.0101</td>
<td>0.0116</td>
<td>0.8649</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td>(1.6108)</td>
<td>(0.0013)</td>
<td>(0.0013)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PSSP T1</td>
<td>5.0761</td>
<td>0.0119</td>
<td>0.0031</td>
<td>3.8142</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>(1.2559)</td>
<td>(0.0010)</td>
<td>(0.0010)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PSSP T2</td>
<td>6.1512</td>
<td>0.0121</td>
<td>0.0055</td>
<td>2.2044</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>(1.5224)</td>
<td>(0.0013)</td>
<td>(0.0012)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)\(\beta_c0\), inverse mean biomass of and individual plant of a crested wheatgrass plant grown in isolation; \(\beta_{cc}\), intraspecific interference for crested wheatgrass; \(\beta_{cn}\), interspecific interference with the seeded native species; \(\beta_{cc}/\beta_{cn}\), relative interference ratio of crested wheatgrass and the seeded native species; \(R^2\), coefficient of determination.

\(^2\)ARTR = sagebrush, ERNA = rabbitbrush, ELEL = squirreltail, and PSSP = bluebunch wheatgrass. T1 and T2 designate Trial 1 and Trial 2, respectively.

\(^3\)Standard errors for coefficients significantly different from zero (P < 0.05). * = not significant.
Table 3-3. Double ratio \([\left(\frac{\beta_{nn}}{\beta_{nc}}\right) : \left(\frac{\beta_{cc}}{\beta_{cn}}\right)\] assessing the resource partitioning based on the seeded native species and crested wheatgrass weight (g).

<table>
<thead>
<tr>
<th>Native Species</th>
<th>([\left(\frac{\beta_{nn}}{\beta_{nc}}\right) : \left(\frac{\beta_{cc}}{\beta_{cn}}\right)]</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARTR T1(^1)</td>
<td>2.4404</td>
</tr>
<tr>
<td>ARTR T2</td>
<td>2.0092</td>
</tr>
<tr>
<td>ERNA T1</td>
<td>4.0544</td>
</tr>
<tr>
<td>ERNA T2</td>
<td>15.9921</td>
</tr>
<tr>
<td>ELEL T1</td>
<td>1.0150</td>
</tr>
<tr>
<td>ELEL T2</td>
<td>1.3299</td>
</tr>
<tr>
<td>PSSP T1</td>
<td>3.7291</td>
</tr>
<tr>
<td>PSSP T2</td>
<td>1.5090</td>
</tr>
</tbody>
</table>

\(^1\) ARTR = sagebrush, ERNA = rabbitbrush, ELEL = squirreltail, and PSSP = bluebunch wheatgrass. T1 and T2 designate Trial 1 and Trial 2, respectively.
CHAPTER 4
CONCLUSION

Crested wheatgrass (Agropyron cristatum [L.] Gaertn.) is one of the predominant seeded species used for rehabilitation of 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 information available for land managers characterizing seed banks and how they function in this system. This research characterized seed bank composition and abundance, and explains some of the factors and mechanisms responsible for variation among seed banks in Wyoming big sagebrush communities historically seeded with crested wheatgrass. The seed banks of seeded Wyoming big sagebrush communities are more dynamic and defined than previously realized. This research challenges the viewpoint that Wyoming big sagebrush communities seeded with crested wheatgrass persist with low floristic and seed bank diversity. Identifying specific mechanisms of succession is critical to gain an understanding of community dynamics (Pickett et al. 1987). Likewise, characterizing seed banks of seeded Wyoming big sagebrush communities will help evaluate, monitor, assess, and make empirical management decisions.

In study one I analyzed and characterized the important species responsible for seed bank differentiation between seeded communities. I also determined what vegetative and soil factors were more likely to be significant contributors to these characterizations. The most significant discovery of my results is that in the absence of fire, herbicide, and mechanical treatments, four different categories were delineated by seed density of the
indicators crested wheatgrass, other grasses, and forbs. These indicators effectively explained 77% of the variation when categorizing the 33 communities. Category 1 had the highest crested wheatgrass seed density and lowest density of all other grasses and forbs. Category 1 also appeared to have the least successional potential due to the absence of an existing native seed bank and the potential interference on native species from the dominance of crested wheatgrass in the seed bank. While many negative and positive feedbacks interact with each other to shape the composition and abundance of seed banks, these feedback need to be further explored to improve management decisions. Increasing the positive feedbacks that reduce resilience in certain communities will help shift the plant community succession toward a more diverse, functional, stabilized ecosystem (Sheley and Krueger-Mangold 2003).

Interference between crested wheatgrass and four important native species at the seedling stage was determined using an addition series, mixed density experimental design in study two (Spitters 1983; Radosevich 1987). The importance of seed and seedling density on intra- and inter-specific interference of native species and crested wheatgrass was evaluated, and resource partitioning between species was characterized. Crested wheatgrass was influenced more by intraspecific competition compared to both shrub species and bluebunch wheatgrass, supporting the general contention that this long-lived perennial grass is more competitive than native species. These three native species were also significantly reduced by crested wheatgrass interference, even though species expressed significant differentiation in resource partitioning. In contrast, interference and resource partitioning coefficients indicated that the native bunchgrass bottlebrush squirreltail equals the competitive ability of crested wheatgrass at the seedling stage.
Thus, the establishment of certain native species can be significantly hindered by high crested wheatgrass seedling and seed banks density, suggesting that rangeland seedings conducted with crested wheatgrass in a mixture with native species or to diversify existing communities may experience considerable interference from crested wheatgrass.

**LITERATURE CITED**


APPENDICES
Table A-1. Summary statistics of the seed bank densities (seeds m\(^{-2}\)) of species for 33 Wyoming big sagebrush communities in the Great Basin. Only abundant species (present in at least 5 communities) were used in analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Communities where Species was Present</th>
<th>Mean</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron cristatum</td>
<td>32</td>
<td>336.87</td>
<td>200</td>
<td>0</td>
<td>1975</td>
<td>78.99</td>
</tr>
<tr>
<td>Ceratocephala testiculata</td>
<td>27</td>
<td>2303.03</td>
<td>325</td>
<td>0</td>
<td>11350</td>
<td>577.33</td>
</tr>
<tr>
<td>Descurainia sophia</td>
<td>27</td>
<td>83.59</td>
<td>50</td>
<td>0</td>
<td>350</td>
<td>16.75</td>
</tr>
<tr>
<td>Poa secunda</td>
<td>24</td>
<td>239.14</td>
<td>50</td>
<td>0</td>
<td>1100</td>
<td>60.90</td>
</tr>
<tr>
<td>Artemesia tridentata</td>
<td>21</td>
<td>49.24</td>
<td>25</td>
<td>0</td>
<td>200</td>
<td>10.35</td>
</tr>
<tr>
<td>Poa bulbosa</td>
<td>19</td>
<td>135.10</td>
<td>25</td>
<td>0</td>
<td>2325</td>
<td>71.69</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>12</td>
<td>105.81</td>
<td>0</td>
<td>0</td>
<td>1700</td>
<td>54.75</td>
</tr>
<tr>
<td>Halogoton glomerotus</td>
<td>10</td>
<td>21.97</td>
<td>0</td>
<td>0</td>
<td>375</td>
<td>11.60</td>
</tr>
<tr>
<td>Hackelia micrantha</td>
<td>10</td>
<td>16.16</td>
<td>0</td>
<td>0</td>
<td>125</td>
<td>5.33</td>
</tr>
<tr>
<td>Alyssum desertorum</td>
<td>8</td>
<td>34.85</td>
<td>0</td>
<td>0</td>
<td>350</td>
<td>15.76</td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>6</td>
<td>44.70</td>
<td>0</td>
<td>0</td>
<td>425</td>
<td>20.05</td>
</tr>
<tr>
<td>Microsteris gracilis</td>
<td>5</td>
<td>16.67</td>
<td>0</td>
<td>0</td>
<td>300</td>
<td>10.07</td>
</tr>
<tr>
<td>Erigeron spp. 1</td>
<td>5</td>
<td>14.65</td>
<td>0</td>
<td>0</td>
<td>375</td>
<td>11.37</td>
</tr>
<tr>
<td>Sisymbrium altissimum</td>
<td>4</td>
<td>5.56</td>
<td>0</td>
<td>0</td>
<td>100</td>
<td>3.28</td>
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<tr>
<td>Sphaeralcea spp.</td>
<td>4</td>
<td>3.28</td>
<td>0</td>
<td>0</td>
<td>33.33</td>
<td>1.58</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>3</td>
<td>19.70</td>
<td>0</td>
<td>0</td>
<td>250</td>
<td>11.08</td>
</tr>
<tr>
<td>Epilobeum halleatum</td>
<td>3</td>
<td>4.55</td>
<td>0</td>
<td>0</td>
<td>100</td>
<td>3.16</td>
</tr>
<tr>
<td>Draba spp.</td>
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<td>168.18</td>
<td>0</td>
<td>0</td>
<td>3325</td>
<td>119.47</td>
</tr>
<tr>
<td>Gayophytum diffusum</td>
<td>2</td>
<td>5.30</td>
<td>0</td>
<td>0</td>
<td>150</td>
<td>4.58</td>
</tr>
<tr>
<td>Lactuca serrida</td>
<td>2</td>
<td>3.03</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>2.11</td>
</tr>
<tr>
<td>Hesperostipa comata</td>
<td>2</td>
<td>1.52</td>
<td>0</td>
<td>0</td>
<td>25</td>
<td>1.05</td>
</tr>
<tr>
<td>Sedge spp.</td>
<td>2</td>
<td>1.52</td>
<td>0</td>
<td>0</td>
<td>25</td>
<td>1.05</td>
</tr>
<tr>
<td>Holosteum umbellatum</td>
<td>1</td>
<td>36.36</td>
<td>0</td>
<td>0</td>
<td>1200</td>
<td>36.36</td>
</tr>
</tbody>
</table>
Table A-1 continued. Summary statistics of the seed bank densities (seeds m\(^{-2}\)) of species for 33 Wyoming big sagebrush communities in the Great Basin. Only abundant species (present in at least 5 communities) were used in analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Communities where Species was Present</th>
<th>Mean</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Vulpia octoflora</em></td>
<td>1</td>
<td>12.88</td>
<td>0</td>
<td>0</td>
<td>425</td>
<td>12.88</td>
</tr>
<tr>
<td><em>Draba cuneifolia</em></td>
<td>1</td>
<td>10.61</td>
<td>0</td>
<td>0</td>
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<td><em>Ericameria nauseosa</em></td>
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<tr>
<td><em>Gilia inconspicua</em></td>
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<tr>
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<tr>
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</tr>
<tr>
<td><em>Phlox pulvinata</em></td>
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</tr>
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</table>

A further 12 dicotyledenous and 1 monocotyledenous species emerged, but died before identification was possible. All unidentified species were rare, occurring on 2 or less communities, and occurred at low densities in the communities.

\(^1\)Nomenclature follows NRCS 2008b.