AN ABSTRACT OF THE DISSERTATION OF

Aleta M. Nafus for the degree of Doctor of Philosophy in Rangeland Ecology and Management presented on June 2, 2015.

Title: Associations Between Crested Wheatgrass and Native Vegetation in Southeastern Oregon: An Investigation of Co-establishment, Environment, Seeding History, and Livestock Management

Abstract approved: ____

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Crested wheatgrass (*Agropyron cristatum* [L] Gaertm), an introduced bunchgrass, has been seeded on over 5 million hectares of degraded rangeland in western North America because it establishes more readily than native bunchgrasses. Because crested wheatgrass stands are associated with native species displacement and low biological diversity, there is substantial interest in re-establishing native species within seeded stands. However, efforts to reintroduce native grasses into crested wheatgrass stands have been largely unsuccessful, and little is known about the long-term dynamics of crested wheatgrass/native species mixes. This project was composed of two studies evaluating interactions between crested wheatgrass and associated native vegetation.

In the first study, I examined the abundance of crested wheatgrass and seven native sagebrush steppe bunchgrasses which had been planted concurrently 13 years prior

at equal densities. Thirteen years after planting, crested wheatgrass was the dominant bunchgrass with a ten-fold increase from its original planted density. Of the seven native bunchgrasses, four species: Idaho fescue (*Festuca idahoensis* Elmer); Thurber's needlegrass *(Achnatherum thurberianum* (Piper) Barkworth); basin wildrye (*Leymus cinereus* (Scribn. & Merr.) A. Löve) and Sandberg bluegrass (*Poa secunda* J. Presl) maintained their low planting density while three species: bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), needle-and-thread *(Hesperostipa comata* (Trin. & Rupr.) Barkworth), and squirreltail (*Elymus elymoides* (Raf.) Swezey), declined in density over the 13-year period. Results suggested that densities of native bunchgrasses planted concurrently with crested wheatgrass were unlikely to increase and that some species only persisted at low levels. However, the continued persistence of native bunchgrasses, even at low densities, suggests that co-planting of some native bunchgrasses may be a viable way of avoiding crested wheatgrass monocultures when this species is necessary for rehabilitation or restoration.

In the second study, I sought to identify environmental, historic and livestock management factors associated with native vegetation occasionally found in seeded crested wheatgrass stands. Basal cover, density, species richness and diversity were measured in 2012 and 2013 on 121 sites previously seeded to crested wheatgrass in southeastern Oregon.

Plant community composition of crested wheatgrass stands was variable; some of the seedings were monocultures of crested wheatgrass while others contained diverse native species. Functional group variability explained by environmental factors ranged from 0% of annual grass density to 56% of large native perennial bunchgrass density. Soil texture was significant and appeared to be an important environmental characteristic explaining functional group cover and density 10-50 years post seeding. Native vegetation was, for all functional groups, positively correlated with soils lower in sand content. Precipitation in the year following seeding of crested wheatgrass has long-term effects on plant community dynamics, especially for Wyoming big sagebrush. Higher precipitation in the year following crested wheatgrass seeding was associated with decreased shrubs, likely because crested wheatgrass seedlings were more successful and therefore sagebrush seedlings experience greater competition.

Moderate grazing was associated with reduced crested wheatgrass monoculture characteristics relative to ungrazed sites. However, within spring grazed and spring-summer grazed sites, there was a negative relationship between increased stocking rate and native species cover and abundance. I speculate that was largely the effect of higher stocking rates being allotted to more productive crested wheatgrass seedings.

Overall, my research suggested that pre-seeding treatment/disturbance on a site appears to have long-term implications for plant community dynamics. However, functional groups varied in response to different pre-seeding treatments. Results support the notion that crested wheatgrass is very competitive with native bunchgrasses in particular; and that introducing natives into crested wheatgrass stands may require high levels of disturbance and may be most successful in more finely-textured soils. The results of this study also suggest that management actions, both at the time of seeding and after seeding, can influence plant community characteristics.

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Associations Between Crested Wheatgrass and Native Vegetation in Southeastern Oregon: An Investigation of Co-establishment, Environment, Seeding History, and Livestock management

by
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A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

Presented June 2, 2015
Commencement June 2015

Doctor of Philosophy dissertation of Aleta M. Nafus presented on June 2, 2015

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

Aleta M. Nafus, Author

ACKNOWLEDGEMENTS

Special thanks go to Dr. Kirk Davies and Dr. Tony Svejcar for everything. I am deeply appreciative of the opportunity to do this project and all the support you guys provided while I did it. I am thankful for all the sage advice, guidance and constructive criticism you provided. I'm thankful to Dr. Kirk Davies for his friendship and continued support. Being his technician and graduate student has been a true pleasure that I will miss as I go forward.

I appreciate my committee, Drs. Mike Borman, Paul Doescher and John Lambrinos for their support and advice. I appreciate everything they contributed to this process and my growth as a scientist.

I will be forever grateful to all the land management personnel who helped me find my study sites and obtain background data. I would particularly like to recognize Jess Wenick (U.S. Fish and Wildlife Service), Randy Wiest (Oregon Department of State Lands) and many BLM personnel, especially Travis Miller, Garry Brown, Pam Keller, Casey O'Connor and Les Boothe without whom this study would have been impossible to implement.

Dr. David Ganskopp made Chapter 2 possible by implementing the study and providing all of his notes on the original plant composition. He also assisted with editing the manuscript. For this I thank him.

I am also indebted to many summer technicians especially Julie Garner, Molly Fitzpatrick, Sarah Fitzpatrick, Brandi Carlon, Kyle Davies and Emily Day who helped dig many holes and count oh so many plants. You guys made even 100+ degree days, plagues of mosquitos and no-see-ums, and miles of dirt roads pleasurable. To you, I offer a mint Tuxedo® salute.

I also appreciate the thoughtful and helpful reviews provided by Drs. David Ganskopp, April Hulet, Erik Hamerlynck and David Pyke as well as anonymous reviewers who helped improve the manuscripts contained within.

And last, but certainly not least, I thank my family who provided hours of encouragement and babysitting, my husband Troy who did so much to help me get here, and the little guy who provided hours of distraction and cuddling whenever I needed a break.

CONTRIBUTION OF AUTHORS

Dr. Kirk Davies and Dr. Tony Svejcar provided guidance during project development, assisted with the development of the sampling protocol and edited the entire Dissertation.

Dr. David Ganskopp originally established the study re-measured for Chapter 2 and provided information about original plant locations. He also edited Chapter 2.

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1 Introduction

1.1 A BRIEF INTRODUCTION OF THE ECOLOGY OF THE SAGEBRUSH STEPPE IN SOUTHEASTERN OREGON

The region of the Northern Basin and Range Ecoregion where my study takes place (Omernik 1987; Soulard 2012; Figure 1.1) has a semiarid climate with cold winters and warm summers. Most of the ecoregion receives less than 38 cm of annual precipitation. The driest areas in the most southeastern corner of the ecoregion receive as little as 19.3 cm and mountain peaks can receive as much as 102 cm annually (Oregon Department of Fish and Wildlife (ODFW) 2006). In most of the ecoregion, peak precipitation often arrives in the late winter months in the form of snow, although some areas receive peak precipitation in the late spring through early summer. The driest months are July – September. Average low temperatures range from -9.6 to -5.7 ˚C (January 1961 - 2000) and average high temperatures range from 30.2 to 35.4 ˚C (July 1961 - 2000) (ODFW 2006). Within the Northern Basin and Range Ecoregion, elevations range from 631 m to more than 2,957 m on Steens Mountain (ODFW 2006).

Potential native vegetation is predominantly sagebrush (*Artemisia L.*) steppe vegetation with juniper (*Juniperus occidentalis* Hook.) woodland on stony uplands (Omernik and Griffith 2014). Sagebrush are widely spaced with an understory of forbs intermixed with cool-season grasses such as Idaho fescue (*Festuca idahoensis* Elmer) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve) (Blaisdell et al. 1982). Within the sagebrush range, mountain big sagebrush (*A. tridentata* spp. *vasyana*) dominates upper elevations, Wyoming big sagebrush (*A. tridentata* spp. *wyomingensis*

(Beetle & A. Young) S.L. Welsh) dominates lower elevations although basin big sagebrush can dominate in valleys and deeper soiled areas. Low sagebrush, (*Artemisia arbuscula* Nutt.), typically dominate on rocky soils high in clay content (Miller et al. 2011).

Wyoming big sagebrush communities historically experienced a low fire frequency with return intervals estimated to occur every 100 – 240 years (Whisenant 1990; Baker 2006; Bukowski and Baker 2012). Wyoming big sagebrush may not recover on a site for more than 30 years following a fire (Wambolt and Payne 1986). Unfortunately, the introduction of annual grasses such as cheatgrass (*Bromus tectorum* L.) has resulted in an increased fire return interval of as little as 3-5 years (Whisenant 1990). This increased fire frequency does not give native perennial vegetation time to recover and instead favors increased annual grass dominance and further increased fire frequency (Whisenant 1990; D'Antonio and Vitousek 1992; Knapp 1996; Chambers et al. 2007). In order to help reduce fire frequency and increase livestock forage, introduced perennial bunchgrasses, such as crested wheatgrass, have been planted in many degraded sagebrush sites.

1.2 INTRODUCTION OF CRESTED WHEATGRASS TO NORTH AMERICA

The crested wheatgrasses (*Agropyron cristatum* [L] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.) are very closely related introduced perennial grasses that have been seeded on over 5 million hectares in semiarid and arid regions of western North America (Mayland et al. 1992). Crested wheatgrass was first introduced to North

America in the late 1800's from Russia (Sharp 1986). Since that introduction, crested wheatgrass has been seeded extensively across North America in an effort to increase livestock forage, decrease wildfires, reduce erosion, and reduce exotic annual grass invasion following disturbance (Dormaar and Smoliak 1985; Young and Evans 1986; Heady 1988; D'Antonio and Vitousek 1992; Sheley and Carpinelli 2005). Since the early 1900's crested wheatgrass has undergone selective breeding to increase its productivity and competitiveness (Carlson and Schwendiman 1986).

Although crested wheatgrass was introduced late in the 1800s, it was not seeded extensively until the 1930's following the massive erosion of topsoil as a result of drought and subsequent abandonment of farms (Sharp 1986). Despite demand for wool and red meat during WWII, widespread rangeland conversion seeding projects were impractical until the late 1940s and early 1950s when a rangeland plow and seeding drill capable of handling the rocks and shrubs were developed (Young and McKenzie 1982). Subsequently, millions of acres were seeded with crested wheatgrass throughout the 1950s and early 1960s (Vale 1974; Pellant and Lysne 2005). In the late 1950s and early 1960s, much of the funding for rangeland restoration and research in the Intermountain West came from the Halogeton Control Bill passed on July 14, 1952. This bill was developed in response to the 1940s discovery that halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.), an exotic, annual species, covered over 2 million acres in eight western states and was responsible for the deaths of thousands of sheep. The bill provided government agencies with funding to seed crested wheatgrass across millions of acres to revegetate the Intermountain West in an effort to combat exotic range weeds such as halogeton that had benefited from biological “near vacuums” caused by widespread overgrazing (Young 1988). Overuse by livestock and a desire to quickly restore depleted rangelands, combined with the idea that sagebrush was reducing forage, led to extensive rangeland rehabilitation projects that were implemented by removing sagebrush and planting crested wheatgrass (Vale 1974; Sharp 1986). Prior to seeding crested wheatgrass, sagebrush was removed using fire, mechanical and chemical treatments (Vale 1974). Once widespread seeding of crested wheatgrass was possible, researchers subsequently set out to investigate grazing systems that would favor crested wheatgrass growth and stand maintenance while minimizing shrub reestablishment (Laycock 1967; Robertson et al. 1970).

Beginning in the 1970s there was increased scrutiny into the use of crested wheatgrass in rangeland restoration projects as people became increasingly concerned about the effects of sagebrush removal and decreased vegetation diversity on the environment, wildlife and sheep livestock production. As a result, public sentiment began to shift towards a preference for a more diverse and native plant community (Vale 1974; Pellant and Lysne 2005). Despite a push towards planting with native species, crested wheatgrass is still seeded in mixes with native species across the Intermountain West following disturbance such as wildfire (Pellant and Lysne 2005; Knutson et al. 2014). Crested wheatgrass is used because it is relatively cost effective, establishes readily, and is highly competitive with undesirable weedy species such as cheatgrass, Russian thistle (*Salsola kali* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski) (Arredondo et al. 1998; Eiswerth et al. 2009; Boyd and Davies 2010; Davies et al. 2010b; James et al. 2011).

1.3 COMPETITION

Two of the main advantages of crested wheatgrass are that it establishes more successfully than natives following revegetation treatments (Boyd and Davies 2010; James et al. 2011) and it is able to out-compete undesirable exotic annuals such as cheatgrass (Arredondo et al. 1998). Once established in an annual grass invaded site, crested wheatgrass can stabilize the soil and hinder further exotic annual grass invasion (Davies et al. 2010b; Davies et al. 2015). Because native vegetation rarely establishes in dense annual grass monocultures, it is believed that crested wheatgrass, if successfully established, opens space into which native grasses can establish (Cox and Anderson 2004). Unfortunately, attempts to restore native perennial grasses into established stands of crested wheatgrass have been largely unsuccessful (Hulet et al. 2010; Fansler and Mangold 2011).

When crested wheatgrass is included in seed mixtures with native species, crested wheatgrass frequently becomes dominant (Heinrichs and Bolton 1950; Schuman et al. 1982; Knutson et al. 2014). This may be, in part, because crested wheatgrass has prolific seed production and can rapidly dominate the seed bank (Marlette and Anderson 1986; Heidinga and Wilson 2002) although it remains relatively unclear as to whether crested wheatgrass excludes natives or if natives just fail to establish. Successfully established native vegetation produces seed, potentially increasing the availability of seed on a site.

Edwards and Crawley (1999) suggest that seed rain is likely critical for maintaining a species. If established native vegetation species coexist with crested wheatgrass they may provide a seed source that allows for continued recruitment, persistence, and even increases of native vegetation in crested wheatgrass communities. Alternatively, because crested wheatgrass frequently dominates the seedbank and is more competitive than many native species at the seedling stage, it may thereby exclude or a least limit the recruitment of native vegetation (Gunnell et al. 2010). Native grass and forb seedlings that do manage to emerge in crested wheatgrass stands face intense competition and most do not manage to establish and persist (Fansler and Mangold 2011).

Crested wheatgrass can not only dominate within a seeded area but can also invade native stands of vegetation adjacent to the seeded areas (Hull and Klomp 1966; Looman and Heinrichs 1973; Marlette and Anderson 1986). This spread into adjacent unseeded areas does not always occur, and may be less likely in more arid environments (Broersma et al. 2000; Krzic et al. 2000). Crested wheatgrass communities can remain a monoculture stand for over 50 years (Hull and Klomp 1966; Looman and Heinrichs 1973; Schuman et al. 1982; Marlette and Anderson 1986) or in other instances some native vegetation, especially sagebrush, may persist (Reynolds and Trost 1981; McAdoo et al. 1989; Grant-Hoffman et al. 2012).

In crested wheatgrass communities, sagebrush is often the most abundant native species (Hull and Klomp 1966; Marlette and Anderson 1986; Krzic et al. 2000; Grant-Hoffman et al. 2012). Crested wheatgrass may inhibit growth of species such as sagebrush (Gunnell et al. 2010) but, once established, sagebrush can occasionally lead to reduced crested wheatgrass seedling survival (Huber-Sannwald and Pyke 2005) with a 3-5% reduction in crested wheatgrass cover for every 1% increase in Wyoming big sagebrush cover (Rittenhouse and Sneva 1976).

1.4 ENVIRONMENTAL FACTORS

1.4.1 Precipitation

There is a positive relationship between crested wheatgrass establishment and precipitation (Shown et al. 1969). Seedings that received an annual average of 25.4 – 30.5 cm of precipitation were generally successful while those receiving less were often unsuccessful (Hull et al. 1962; Reynolds and Springfield 1953; Plummer et al. 1955). The effect of precipitation on seeding success may be influenced by temperature and soil texture. On sites where temperatures are moderate and soils are permeable, crested wheatgrass can successfully establish with only 20.3 cm of annual precipitation (Shown et al. 1969). Good precipitation may be especially important to the success of crested wheatgrass seedings in the first and second year post-seeding while crested wheatgrass plants are developing a vigorous root system (Shown et al. 1969). In areas where a seed source is available, sagebrush and rabbitbrush (*Chrysothamnus viscidiflorus (Hook.) Nutt.*, *Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird*) may be able to establish in crested wheatgrass during years with good precipitation (Frischknecht and Harris 1968) especially in the first two or three years post-seeding (Heady and Bartolome 1977).

1.4.2 Soils

Soil texture may be one of the most important environmental characteristics related to the abundance of native vegetation on sites seeded with crested wheatgrass. Soil texture has previously been found to be highly correlated to cover and diversity of native plants with higher cover and diversity of native plants in soils higher in silt and clay (Raven 2004; Davies et al. 2007a; Williams 2009). Although sandy sites tend to be associated with higher crested wheatgrass and lower native herbaceous cover, shrub species such as Wyoming big sagebrush may be able to establish allowing for at least some diversification of the site (Shown et al. 1969; Williams 2009).

1.4.3 Topography

Southern exposures typically dry out more rapidly than north facing slopes leading to higher vegetative water stress (Hinds 1975) and potential differences in species composition. Cheatgrass is more likely to dominate south facing slopes while Sandberg bluegrass (*Poa secunda* J. Presl) is more likely to occur on north facing slopes (Link et al. 1990).

1.5 MANAGEMENT

1.5.1 Seedbed Preparation and Seeding

Historically, sagebrush communities were often targeted for conversion to crested wheatgrass stands. Prior to seeding, sagebrush stands were generally treated by burning, by spraying with a broadleaf herbicide, such as 2,4-D or with mechanical treatments such as plowing, chaining, or mowing (Hull and Klomp 1974; Vale 1974; Heady and Bartolome 1977; Cluff et al. 1983). Aerial spraying of herbicides can kill up to 99% of sagebrush (Pechanec et al. 1965; Wambolt and Payne 1986) but sagebrush mortality may be variable depending on soil type and available soil moisture (Cluff et al. 1983). For example, sagebrush mortality is higher on sites with sandy or gravelly soils and lower on sites high in silt or clay (Cluff et al. 1983) and is dependent on soil moisture being available (Cook 1963; Cluff et al. 1983). The success of plowing to control sagebrush is highly variable depending on soil type. Plowing moist, coarse-textured soil killed most sagebrush whereas heavy compact soils required plowing twice to control sagebrush (Pechanec et al. 1965; Cluff et al. 1983)

Crested wheatgrass is typically seeded either by airplane broadcasting of pelleted or unpelleted seed or by using a rangeland drill to distribute seeds in furrows (Hull and Klomp 1967; Young and McKenzie 1982). Crested wheatgrass was originally seeded in a monoculture or with other introduced forage species such as alfalfa (*Medicago sativa* L.) but is now typically seeded as part of a seed mix containing native and introduced species (Pellant and Lysne 2005).

1.5.2 Fire

Crested wheatgrass burns quickly with little heat transfer into the soil and is therefore more resilient to fire than many native bunchgrass species (DePuit 1986; Skinner and Wakimoto 1989). Although spring burning decreases crested wheatgrass production for several years, post-fire recovery of crested wheatgrass is generally rapid, especially if fire occurs in the late summer (Young 1983; Bradley et al. 1992). Fall burning may reinvigorate a stand of crested wheatgrass (Lodge 1960).

Sagebrush is readily killed by fire although some plants may survive in rocky outcroppings and provide a seed source for later establishment (Skinner and Wakimoto 1989; Ziegenhagen and Miller 2009). The reduction in sagebrush competition post-fire can lead to a 3-6 fold increase in crested wheatgrass within three years (Ralphs and Busby 1979). Frequent fire is often associated with increased rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt., *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird) density (Bunting et al. 1987) but fire can also cause significant rabbitbrush mortality and reduced rabbitbrush presence on the site (Bunting 1989).

1.5.3 Grazing

Early research into grazing crested wheatgrass was devoted to the goal of maintaining crested wheatgrass and reducing the reestablishment of shrubs (Cook et al. 1958; Hull and Klomp 1966; Frischknecht and Harris 1968; Hull 1974). In theory, we can now utilize this research in reverse to determine which livestock grazing practices might best encourage native vegetation establishment into stands of crested wheatgrass.

Livestock grazing practices can influence plant community dynamics of a crested wheatgrass stand. Intensity, duration, season and animal type all influence plant succession. Crested wheatgrass is very tolerant to grazing and can withstand heavy grazing for multiple years (Cook et al. 1958; Hull and Klomp 1966; Hull 1974; Caldwell et al. 1981; Laycock and Conrad 1981). Heavy autumn grazing favors crested wheatgrass dominance and minimal sagebrush encroachment relative to spring grazing since grazing crested wheatgrass while it is dormant reduces its “wolfiness” and increases its productivity in the spring (Frischknecht and Harris 1968; Robertson et al. 1970; Hull and Klomp 1974; Laycock and Conrad 1981). Grazing methods that disfavor crested wheatgrass such as spring grazing, especially during drought, or high-intensity, long duration grazing tend to promote shrub establishment, especially when grazers, such as cattle, tend to prefer herbaceous vegetation and avoid shrub species (Robertson et al. 1970; Laycock and Conrad 1981; Salihi and Norton 1987; Olson and Richards 1988; Busso and Richards 1995; Angell 1997). Herbivores that significantly browse, such as sheep, are less likely to promote shrub establishment (Owens and Norton 1992). Heavy grazing may facilitate the reintroduction of grazing tolerant native species (i.e sagebrush, Sandberg bluegrass, needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) although it hinders more sensitive species such as bluebunch wheatgrass (Hyder and Sawyer 1951; Krzic et al. 2000). Heavy grazing of crested wheatgrass can also contribute to undesirable weed invasion (Bleak and Plummer 1954; Frischknecht and Harris 1968).

1.6 FIGURES

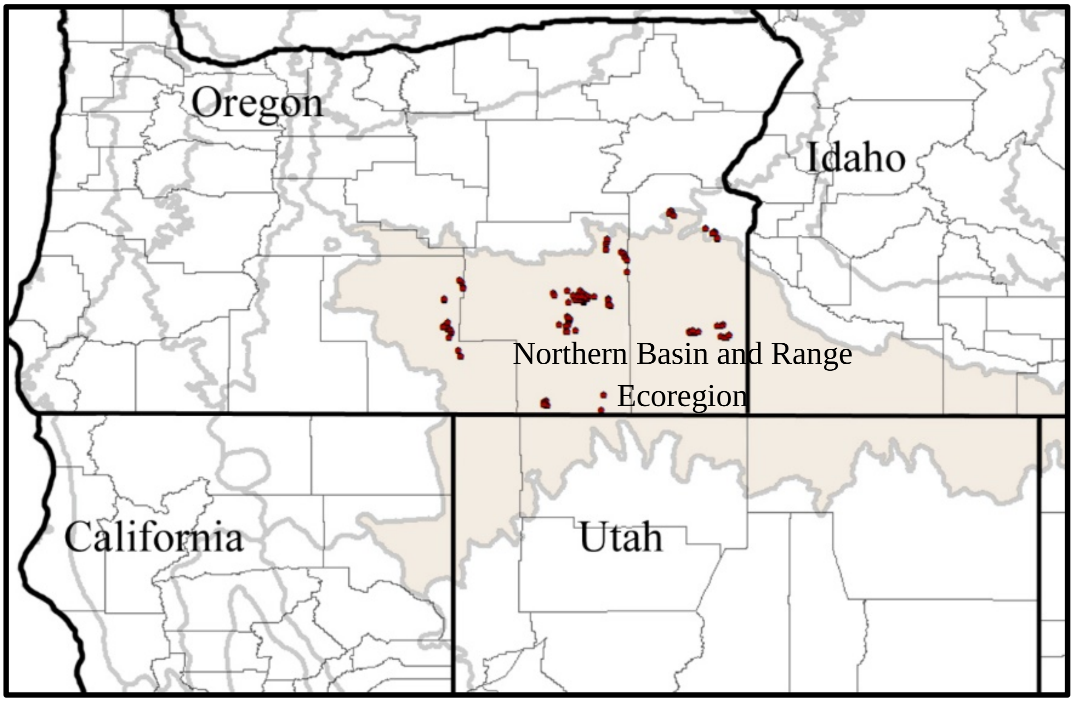

Figure 1.1. Study locations (red circles) were located in a 54230-km^2 area in southeastern Oregon within the Northern Basin and Range Ecoregion (Soulard 2012; U.S. Environmental Protection Agency 2013).

2 Abundances of co-planted native bunchgrasses and crested wheatgrass after 13 years

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Rangeland Ecology and Management
Volume 68(2): 211–214 (2015)

2.1 ABSTRACT

Crested wheatgrass (*Agropyron cristatum* [L] Gaertm) has been seeded on over 5 million hectares in western North America because it establishes more readily than native bunchgrasses. Currently, there is substantial interest in re-establishing native species in sagebrush steppe, but efforts to reintroduce native grasses into crested wheatgrass stands have been largely unsuccessful, and little is known about the long-term dynamics of crested wheatgrass/native species mixes. We examined the abundance of crested wheatgrass and seven native sagebrush steppe bunchgrasses planted concurrently at equal low densities in non-grazed and unburned plots. Thirteen years post-establishment, crested wheatgrass was the dominant bunchgrass, with a ten-fold increase in density. Idaho fescue (*Festuca idahoensis* Elmer), Thurber's needlegrass *(Achnatherum thurberianum* (Piper) Barkworth), basin wildrye (*Leymus cinereus* (Scribn. & Merr.) A. Löve) and Sandberg bluegrass (*Poa secunda* J. Presl) maintained their low planting density, whereas bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), needle-and-thread *(Hesperostipa comata* (Trin. & Rupr.) Barkworth), and squirreltail (*Elymus elymoides* (Raf.) Swezey) densities declined. Our results suggest that densities of native bunchgrasses planted with crested wheatgrass are unlikely to increase and that some species may only persist at low levels. The persistence of native bunchgrasses suggests that co-planting of some native bunchgrasses may be a viable way of avoiding crested wheatgrass monocultures when this species is necessary for rehabilitation or restoration.

Key Words: *Agropyron cristatum*, restoration, revegetation, sagebrush steppe,

2.2 INTRODUCTION

Crested wheatgrasses, *Agropyron cristatum* [L] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.), have been seeded on over 5 million hectares across semiarid and arid western North American rangelands (Maryland et al. 1992). In the Intermountain West, crested wheatgrass is often seeded in mixes with native species (Pellant and Lysne 2005). It is relatively cost effective, establishes readily, and, as it is highly competitive with undesirable weedy species (Arredondo et al. 1998; Eiswerth et al. 2009), may facilitate establishment of more desirable native vegetation (Cox and Anderson 2004). However, the competitive nature of crested wheatgrass can result in monoculture stand formation and seed bank domination (Pyke 1990), which can both hinder establishment of native species (Marlette and Anderson 1986; Gunnell et al. 2010) and induce native species displacement and low biological diversity (Christian and Wilson 1999; Krzic et al. 2000; Vaness and Wilson 2007). When crested wheatgrass is included in seed mixtures with native species, crested wheatgrass frequently becomes dominant (Heinrichs and Bolton 1950; Schuman et al. 1982; Knutson et al. 2014); however, it remains relatively unclear as to whether crested wheatgrass excludes natives or if natives just fail to establish. Efforts to remove crested wheatgrass and re-seed natives rarely increases native vegetation establishment (Hulet et al. 2010; Fansler and Mangold 2011). Native herbaceous vegetation has successfully reestablished in some crested wheatgrass communities (Williams 2009), however, since most studies are shorter than five years, little is known about the ability of established native bunchgrasses to coexist with crested wheatgrass more than a decade after planting.

Successfully established native vegetation produces seed, potentially increasing the availability of seed on a site. Edwards and Crawley (1999) suggest that seed rain is likely critical for maintaining a species. If established native vegetation species coexist with crested wheatgrass they may provide a seed source that allows for continued recruitment, persistence and even increases of native vegetation in crested wheatgrass communities. Alternatively, because crested wheatgrass frequently dominates the seedbank and is more competitive than many native species at the seedling stage, it may thereby exclude or a least limit the recruitment of native vegetation (Gunnell et al. 2010). Therefore, more information is needed on the potential likelihood of native bunchgrasses species to maintain their presence the community after co-establishment with crested wheatgrass.

To evaluate the long-term response of native perennial bunchgrasses when co-planted with crested wheatgrass we looked at bunchgrass species abundance 13 years after simultaneous planting. We hypothesized that the density of each native bunchgrass species would decrease over time, and that crested wheatgrass would become the dominant bunchgrass.

2.3 METHODS

2.3.1 Study area

The study site is located on the Northern Great Basin Experimental Range (lat 43 28'48.3"N, long -119 42'32.2"W, elev 1 403 m) 56 km west of Burns, Oregon. Average annual precipitation at the site is 286 mm, typically arriving as snow or rain from October to March (data file, Eastern Oregon Agricultural Research Center, Burns, OR). Soils at the site are a complex of loam and loamy fine sands (Milican coarse-loamy, mixed, frigid Orthidic Durixerolls and Holte coarse-loamy, mixed, frigid Orthidic Haploxerolls, respectively (Lentz and Simonson 1986; Ganskopp et al. 2007). Depth to bedrock or hardpan ranged from 90-150 cm (Ganskopp et al. 2007).

Vegetation in neighboring pastures is characterized by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle) overstory with a diverse understory that contained all of the native bunchgrasses evaluated in this study.

2.3.2 Experimental Design

In 1989, nine 313 m^2 plots were established in a site cleared of vegetation for a paddock study using methods outlined in Cruz and Ganskopp (1998) and Ganskopp et al. (2007). Seven native bunchgrass species, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), basin wildrye (*Leymus cinereus* (Scribn. & Merr.) A. Löve), Idaho fescue (*Festuca idahoensis* Elmer), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), needle-and-thread *(Hesperostipa comata* (Trin. & Rupr.) Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), and Thurber's needlegrass *(Achnatherum thurberianum*

(Piper) Barkworth) and one introduced bunchgrass species, ‘Nordan’ crested wheatgrass, were transplanted into each plot as mature plants harvested from nearby plant communities. The bunchgrass species were planted so that each plot contained 2.6 total plants or 0.33 plants per species·m^{-2} randomly assigned to an evenly spaced grid of 29 rows and 29 columns (resulting in 841 cells) with plants positioned at the center of each cell such that there were 0.61 m between plant centers. This resulted in a total of 800 (100 per species) planted cells and 41 randomly distributed empty cells in each plot. In 1998, the site was weeded and restocked with transplants from nearby communities when necessary to achieve original plant densities (Ganskopp et al. 2007). Except for the 1998 experiment (Ganskopp et al. 2007), domestic livestock grazing were excluded since 1989. Since the last treatment in 1998; the communities were left to the natural processes of recruitment and mortality.

2.3.3 Vegetation measurement and statistical analyses

In 2011, we recreated the original grid described above and counted, by species, the bunchgrasses in each plot. To determine whether there was a change in species abundance over time we used repeated measures multivariate analysis of variance (MANOVA) with density in 1998 and density in 2011 as response variables and species as an independent variable in JMP 10.0.2. To determine which species were different, we used a pairwise comparison with the Tukey HSD adjustment obtained using an analysis of variance (ANOVA) on the change in abundance grouped by species in R (version 3.0.2; R Core Team 2013). This change in abundance was the 1998 abundance subtracted from the 2011 abundance. In order to determine the effect of time on individual species we used a one sample two-tailed t-test to compare the 2011 abundance of each species to the null starting (1998) abundance using R (version 3.0.2). Results were reported as density·m^{-2}. Abundance data was normally distributed and a transformation was not used. Means were reported with standard error of means (SE). For the t-tests, significance was set at a conservative $P < 0.006$ (0.05/8) to reduce the chance of type I error. All P-values refer to t-test results unless otherwise indicated.

2.4 RESULTS

The MANOVA revealed a significant effect for the interaction of species and time (F (7, 64) = 29.5, p <. 001). Given the significance of the overall test, an ANOVA was used to examine the change in species abundance which showed there was *an* increase in total bunchgrass density from 2.64 plants·m^{-2} (8 species at *0.33* plants·m^{-2} each) in 1998 to 5.23 $\pm$ 0.02 plants·m^{-2} in 2011 ($P < 0.001$, $F (7, 64) = 260.0$). The Tukey pairwise comparison revealed that *c*rested wheatgrass had the greatest increase in density in the community: a ten-fold increase in density over the 13-year period (3.37 $\pm$ 0.35 plants·m^{-2}; $P < 0.001$; Fig. 1). Crested wheatgrass composed 64% of the total bunchgrass abundance. The native bunchgrasses each contributed between 3 to 8% of the remaining bunchgrass abundance. Idaho fescue was the only native grass that slightly increased in density, by about 0.1 plants m^2 to 0.43 $\pm$ 0.13 plants·m^{-2}. However its response was highly variable (Fig. 1) and was not strongly statistically significant ($P = 0.07$). Thurber's needlegrass, Basin wildrye and Sandberg bluegrass maintained a similar density over time (0.28 $\pm$

0.08, 0.26 $\pm$ 0.04, and 0.32 $\pm$ 0.20, respectively; $P > 0.01$; Fig. 1). In contrast, squirreltail, needle-and-thread and bluebunch wheatgrass decreased over the 13 year study interval (0.17 $\pm$ 0.07, 0.20 $\pm$ 0.03, and 0.19 $\pm$ 0.06 plants$\cdot$m^{-2}, respectively; $P \leq 0.001$; Fig. 1), with *s*quirreltail experiencing the greatest decline (ca. 50%).

2.5 DISCUSSION

As we hypothesized crested wheatgrass became dominant in the community after 13 years. Similar to other, more short-term studies (see Heidinga and Wilson 2002; Grant-Hoffman et al. 2012), we found that crested wheatgrass rapidly became the most abundant bunchgrass in the mixed grass community, and increases in crested wheatgrass were often; though not always, associated with declines in native grasses. The presence of established native species, may reduce the extent of crested wheatgrass dominance (Bakker and Wilson 2004), potentially slowing the recruitment of crested wheatgrass into the community. The relatively stable density of Idaho fescue, Thurber's needlegrass, Basin wildrye and Sandberg bluegrass over our 13 year study suggests that these species may persist in sagebrush steppe when co-planted with crested wheatgrass, especially at our elevation and sparse planting densities. Other studies have found that Sandberg bluegrass is less negatively impacted by the presence of crested wheatgrass than other species (e.g. bluebunch and needle-and-thread grass) and can coexist with crested wheatgrass (Broersma et al. 2000; Heidinga and Wilson 2002; Henderson and Naeth 2005) possibly because it grows and senesces earlier than other bunchgrasses (James et al. 2008), which may allow it to avoid competition for scarce moisture resources.

It is difficult to determine whether those species that showed declines in density (squirreltail, needle-and-thread, bluebunch wheatgrass) will simply have a decreased presence in the community or whether declines will lead to their eventual extirpation. Similar to our results, Henderson and Naeth (2005) found that bluebunch wheatgrass decreased when it coexisted in communities with crested wheatgrass. Squirreltail also tends to be negatively correlated with crested wheatgrass abundance (Davies et al. 2010b; Grant-Hoffman et al. 2012) despite its greater ability to effectively compete with crested wheatgrass at the seedling stage than other native bunchgrasses (Gunnell et al. 2010). We found that crested wheatgrass appears to be filling available open spaces while the density of native bunchgrasses remained static or decreased slightly. Perennial bunchgrasses in our study sites were spaced at even distances from one another and at relatively low densities. This is a stark contrast to the clumping of bunchgrasses in drill rows with drill seeding, which may alter plant community dynamics. The ability of crested wheatgrass to recruit high numbers of individuals relative to native bunchgrasses in co-planted communities means that even if native bunchgrasses are established into existing stands of crested wheatgrass, their presence is unlikely to increase in the community. The dominance of crested wheatgrass suggests that efforts to diversify crested wheatgrass stands with native bunchgrasses may not be successful without significant and lasting control of crested wheatgrass. Knutson et al. (2014) found evidence suggesting that planting native bunchgrasses is most successful when crested wheatgrass is not included in the seed mixture. When native species do successfully establish with crested wheatgrass, they often decrease within three years (Davies 2010; Hulet et al. 2010; Fansler and Mangold 2011). However, despite decreases in some species, migration of the co-planted native bunchgrasses into neighboring cells suggests that they were recruiting into the plant community; even if at low levels, and so may maintain a presence in the community. Presence of larger native species may be underestimated in our study since cover or plant size was not measured and species like Basin wildrye have a stronger presence than density can indicate. The high recruitment of crested wheatgrass helps explain why its presence can limit exotic annual grasses, especially in wetter, cooler environments such as our study site (Knutson et al. 2014), and why, in some situations, crested wheatgrass may be selected for seeding when the goal is to reduce the risk of exotic annual grass invasion and dominance, particularly following a wildfire event (Davies 2010).

Although our experiment is replicated at one site only, it is a valuable contribution to our understanding of the relationship between crested wheatgrass and native perennial bunchgrasses as there are few studies with a similar combination of duration and experimental control. Our study provides a unique opportunity to examine long-term changes in abundance of native bunchgrasses established alongside crested wheatgrass in the sagebrush steppe. Longer-term monitoring will be necessary to determine whether the community maintains its diversity, or eventually converts to a near monoculture stand of crested wheatgrass. Further evaluations at sites with varying site and climatic characteristics may help identify the species that are more likely to effectively coexist with crested wheatgrass across its seeded range.

2.6 MANAGEMENT IMPLICATIONS

The 10-fold increase in crested wheatgrass density and decrease in half of the native bunchgrass species raise the question of how effective simultaneous seedings of crested wheatgrass and native bunchgrasses will be if the management objective is for native vegetation to establish and increase. Some native bunchgrass species, in our case, Sandberg bluegrass, Thurber's needlegrass and Idaho fescue, may be more likely to maintain a presence in the community, though the most suitable species will likely also differ depending on site characteristics. We had an evenly dispersed, low-density planting which may reduce competitive interactions compared to a more typical seeding where plants tend to emerge at higher densities. If crested wheatgrass is needed to reclaim a site or reduce exotic annual grass invasion, it may be an ineffective use of resources to seed those native bunchgrass species that are less likely persist over long time periods. Our results suggest that if native bunchgrasses are likely to establish and meet management objectives, it may be undesirable to include crested wheatgrass as it will likely increase at greater rates than native bunchgrasses.

2.7 ACKNOWLEDGMENTS

The authors thank J. Garner, S. Fitzpatrick, S. Duff, R. Johnson and B. Carlon for their assistance with data collection. We are grateful to April Hulet and Erik Hamerlynck for reviewing earlier revisions of this manuscript. We also appreciate the thoughtful reviews of anonymous reviewers.

2.8 FIGURES

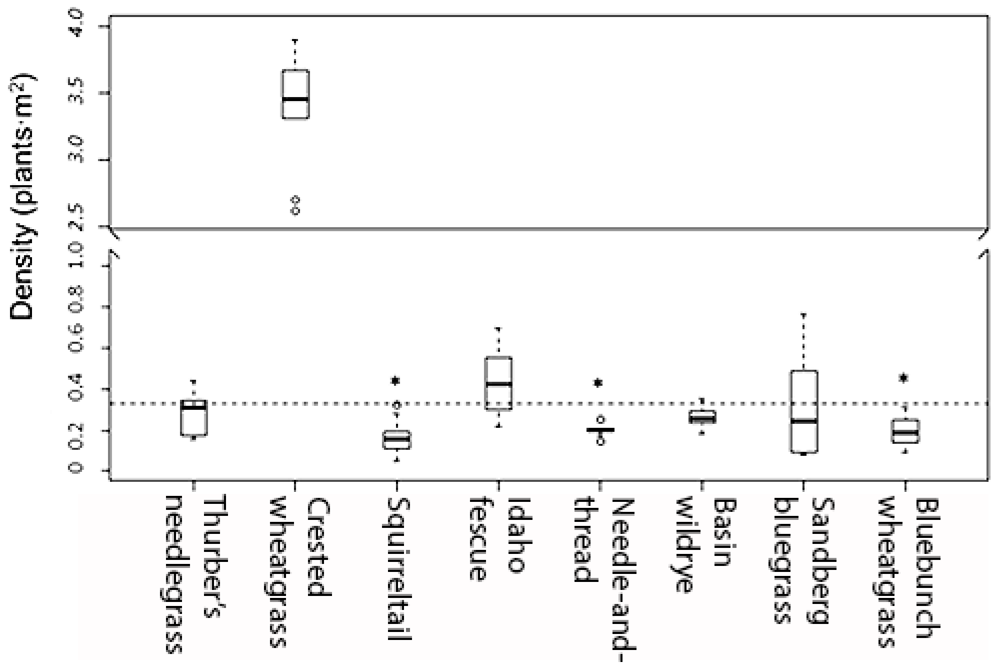

Figure 2.1. Average density of perennial bunchgrasses in 2011. Starting density was 0.33 plants m·$^{-2}$ in 1998 (dashed line). Asterisk indicates a statistically significant (P < 0.05) difference in density between 1998 and 2011. Note scale change on y axis below solid reference line.

3 Environmental Characteristics Associated with Native Vegetation Variability in Introduced Bunchgrass Stands

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For submission to Plant Ecology or Journal of Arid Environments

3.1 ABSTRACT

Crested wheatgrass, an introduced bunchgrass seeded across western North America, is often associated with native species displacement and low biological diversity. However, there is a lack of information about native vegetation variability in crested wheatgrass stands. We sought to better understand the range of native vegetation in areas seeded with crested wheatgrass and to identify correlations between environmental characteristics and native vegetation. We measured basal cover, density, species richness and diversity on 121 sites that spanned a 54230-km^2 area in southeastern Oregon. We used mixed model selection in multiple linear regression to identify environmental factors that best explained variability of functional group cover and density, and species richness and diversity. Plant community composition of crested wheatgrass stands was variable; some seedings were a monoculture of crested wheatgrass while others contained diverse native species assemblages with large numbers of native vegetation, especially shrubs. Environmental factors explained a range of functional group variability from 0% of annual grass density to 56% of large native perennial bunchgrass density. Soil texture was significant in all best regression models, and appeared to be an important environmental characteristic explaining functional group cover and density. Native vegetation was, for all functional groups, positively correlated with soils lower in sand content. Our results suggest environmental differences explain a large amount of the variability of native vegetation in crested wheatgrass stands, and this information will be useful in assessing the potential for native vegetation to co-occupy sites seeded with

crested wheatgrass. This research also suggests that seeding crested wheatgrass does not always result in monocultures as many seedings contained a diverse assemblage of native vegetation.

3.2 INTRODUCTION

Crested wheatgrass and desert wheatgrass (*Agropyron cristatum* (L.) Gaertn. and *Agropyron desertorum* [Fisch.] Schult.); hereafter referred to as crested wheatgrass are closely-related introduced perennial grasses that have been extensively seeded across western North America in an effort to increase livestock forage, decrease wildfires and to reduce erosion and exotic annual grass invasion following disturbance (Dormaar and Smoliak 1985; Young and Evans 1986; Heady 1988; D'Antonio and Vitousek 1992; Sheley and Carpinelli 2005). Crested wheatgrass is often selected for seeding because it is more cost-effective and establishes more readily than many native species (Boyd and Davies 2010; James et al. 2012; Davies et al. 2015).

Crested wheatgrass is a strong competitor, and may form monoculture stands leading to concerns about native species displacement and low biological diversity (D'Antonio and Vitousek 1992; Christian and Wilson 1999; Krzic et al. 2000). Native species may not disperse well into stands of crested wheatgrass (Marlette and Anderson 1986) and crested wheatgrass is more likely than native bunchgrasses to fill open safe sites (Nafus et al. 2015). Native seedlings that do emerge in crested wheatgrass stands face intense competition and most do not establish and persist (Fansler and Mangold 2011). Crested wheatgrass can remain a monoculture stand for over 50 years (Hull and Klomp 1966; Looman and Heinrichs 1973; Marlette and Anderson 1986) or, in some instances, revert to sagebrush (*Artemisia* L.) dominance (Reynolds and Trost 1981; McAdoo et al. 1989).

It is not clear why native vegetation occurs in some crested wheatgrass seedings but not in others. Many factors are likely important including pre-seeding community composition and health, seeding success, environmental site characteristics and post-seeding management. Environmental characteristics that may influence vegetative composition including soil texture, soil nutrients, soil pH, rockiness, climate, and landscape characteristics like aspect, slope and elevation (Shown et al. 1969; Hinds 1975; Heady 1988; Link et al. 1990; Raven 2004; West and Yorks 2006; Williams 2009). Soil texture may be one of the most important environmental characteristics related to the abundance of native vegetation on sites seeded with crested wheatgrass as cover and diversity of native plants are positively correlated with soils higher in silt and clay (Raven 2004; Davies et al. 2007a; Williams 2009).

Factors that are associated with greater presence of native vegetation in established stands of crested wheatgrass are of interest because efforts to seed native vegetation into stands of crested wheatgrass are largely unsuccessful even when crested wheatgrass is controlled prior to seeding (Hulet et al. 2010; Fansler and Mangold 2011). In addition, there is disagreement over the use of crested wheatgrass with proponents stating that natives can co-exist with crested wheatgrass and opponents stating that it decreases diversity and displaces native vegetation (Pellant and Lysne 2005; Davies et al. 2011). Thus, there is a critical need for information on the range of plant community characteristics of crested wheatgrass stands especially since management goals often have an emphasis on increasing species diversity (Pellant and Lysne 2005).

Our objective was to identify environmental factors correlated with native plant density, cover, richness, and diversity and quantify the variability in native vegetation characteristics on sites seeded with crested wheatgrass. We hypothesized that native vegetation cover and density would be positively correlated with finer textured soils, higher elevation and greater site rockiness and that sites with finer textured soil would have higher species diversity and richness.

3.3 METHODS

3.3.1 Study area description

One hundred and twenty one study sites were selected across 54230 km^2 in southeastern Oregon (Figure 3.1). Study locations were generally in Wyoming big sagebrush-bunchgrass ecological sites though a few locations were more alkaline and had been characterized by shrubs such as spiny hopsage (*Grayia spinosa* (Hook.) Moq.) and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). All study locations were seeded with crested wheatgrass 10 to 50 years prior using drill and aerial seeding methods. Long-term mean annual precipitation for study locations ranged between 200 and 360 mm (with one location at 460 mm) (PRISM Climate Group 2014). Annual precipitation amounts (from 1 October to 30 September) for study locations were 74% of the long-term average (30 years) in 2011-2012 and 75% of the long-term average in 2012-2013. Precipitation in this region arrives mainly as snow from November to March.

3.3.2 Site selection

Expert personnel from the U.S. Department of Interior Bureau of Land Management (BLM) of the Burns, Lakeview, and Vale BLM Districts and the U.S. Fish and Wildlife Service were consulted to obtain locations of all crested wheatgrass seedings in their jurisdiction. One hundred and twenty-one sites were located and measured in June-August 2012 and 2013. With the advice of land managers, we selected seedings and sampled multiple locations within each seeding and across a gradient of environmental conditions to capture a range of crested wheatgrass dominance and variability of native vegetation. All sites sampled had been identified as having been seeded with crested wheatgrass and contained at least 0.25 crested wheatgrass plants per m^2 to ensure that they had been successfully seeded.

3.3.3 Vegetation characteristics

A 50 x 60-m plot was used to sample each of the 121 sites. Four parallel 50-m transects were located at 20-m intervals along the 60-m side of the plot. Annual and perennial herbaceous vegetation basal cover and density were estimated by species inside 40 x 50-cm quadrats located at 3-m intervals on each 50-m transect (starting at 3 m and ending at 45 m), resulting in 15 quadrats per transect and 60 quadrats per plot. Ground cover (bare ground, rock, litter and crypto-biotic crust) were also estimated in the 40 x 50-cm quadrats. Basal cover was estimated to the nearest 1% based on markings that divided the quadrat into 1, 5, 10, 25, and 50% segments. We used basal cover as opposed to foliar cover as many sites were grazed prior to sampling. Individual plants were counted for abundance if at least 50% of the plant was rooted in the quadrat. Bunchgrasses were considered separate individuals if there were more than 5 cm between clumps. Sandberg bluegrass individuals were considered as separate if there was more than 1 cm between clumps. Dead portions of the crown were included in the basal cover estimate when they were not more than 5 cm across and were within the perimeter of the live portion. Shrub canopy cover by species was measured using the line intercept method (Canfield 1941). Canopy gaps less than 15 cm were included in canopy cover estimates. Shrub density was determined by counting all individuals rooted in four, 2 x 50-m belt transects at each plot. Each 2 x 50-m belt transect was centered over one of the four 50-m transects. Cover and density were summarized by species for each plot. Species were subsequently summarized by functional group: large native perennial bunchgrasses; perennial forbs, annual grasses, annual forbs, and shrubs. Crested wheatgrass and Sandberg bluegrass (*Poa secunda* J. Presl), however, were analyzed separately. Sandberg bluegrass was classified as a separate functional group because of its relatively small stature and early development compared to other perennial bunchgrasses in these plant communities (James et al. 2008) and because it tends to respond more favorably to grazing pressure than many other native sagebrush steppe bunchgrasses (Robertson 1971). As the only non-native bunchgrass, crested wheatgrass was classified as a separate functional group. Functional groups were used because they are a common ecological method for grouping species that are expected to have similar temporal or spatial resource acquisition patterns and it simplifies comparisons among plant communities with different species composition (Boyd and Bidwell 2002; Davies et al. 2007b). Species richness was determined by summing all species found in the quadrats at each site. Vegetation diversity was calculated from species density measurements using the Shannon-Weiner diversity index (Krebs 1998). Wyoming big sagebrush was included in the shrub functional group but was also evaluated independently because of its importance to the habitat requirements of many sagebrush-associated wildlife species (Davies et al. 2011).

3.3.4 Environmental factors

A total of 14 environmental variables were measured at each site (Table 3.1). One 0-15-cm and one 15-60-cm soil sample were collected at the center of the plot in the open spaces between vegetation. Two additional 0-15-cm samples were collected, one at 15 m NW and one at 15 m SW from the center of the plot. Prior to collection, any surface litter was removed. If it was not possible to reach 60 cm, the depth attained was recorded. From the side of each hole, a 5-cm wide vertical sliver was collected from 0-15 cm and, in the center hole, from 15-60 cm. Samples were placed in separate bags by depth and location and air dried for further analysis. Soil texture was estimated using the hydrometer method (Bouyoucos 1962). Soil pH from the 0-15 cm soil samples was determined by mixing 5-mg soil samples with 15 mL nanopure H_20, agitating for 5 minutes and allowing to settle for 45 minutes, then stirring vigorously immediately prior to inserting a Beckman 3 in 1 pH probe (Beckman Coulter, Inc, Brea, CA.) into the solution. The carbon and nitrogen concentration for each 0-15 cm soil sample were determined by oven drying and combusting samples using a LECO CN 2000 (LECO

Corp., St. Joseph, MI). The values for the three 0-15 cm depth samples were averaged into a single plot value. Locational coordinates (decimal degrees), slope (degrees), aspect and elevation (m) were recorded at each site. Longitude, aspect and slope were used to calculate heat load (McCune and Keon 2002).

Precipitation was estimated for each site using the Precipitation-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2014).

3.3.5 Statistical analyses

Crested wheatgrass cover and density was regressed against species richness, species diversity and each of the functional group and Wyoming big sagebrush cover or density (JMP 10.0.2). Step-wise multiple linear regression (JMP 10.0.2) was used to select models correlating basal cover and density of functional groups and species diversity and richness with environmental factors. Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPG), annual grasses, perennial forbs, annual forbs, shrubs, Wyoming big sagebrush, Shannon-Weiner diversity (H') and species richness were used as response variables to perform step-wise multiple linear regression model selection. Environmental variables (Table 3.1) were added and deleted in stepwise fashion using p-values to select a parsimonious model that explained the most variation in the response variables resulting in the highest adjusted R^2 value. Environmental factors that did not contribute significantly ($p \geq 0.05$) were excluded from the final model. Because latitude, aspect and slope were included in the calculation of heat load index, they were not used independently for model selection. Data were square root transformed prior to model selection when necessary to better meet linear regression data distribution assumptions. Parametric statistics were used to describe vegetation characteristics of crested wheatgrass stands. Means were reported with standard errors.

3.4 RESULTS

Annual forbs occurred in 93%, annual grasses in 89%, Sandberg bluegrass in 85%, shrubs in 81%, large native perennial forbs in 75%, and large native perennial bunchgrasses (LNPB) in 59%, of the 121 sites sampled. One site contained only crested wheatgrass and a few greasewood plants, while the rest of the sampled sites contained at least 3 plant species with at least one native species and over half of the sites contained at least 14 plant species. Total species richness, including shrub and herbaceous species, ranged between 2 and 37 species averaging 13.2 $\pm$ 0.8 species per site with perennial herbaceous species averaging 6.5 $\pm$ 0.4 (Figure 3.3). Total species diversity, including shrub and herbaceous species, ranged from 0.002 to 2.23; with total herbaceous and herbaceous perennial species diversity averaging 1.1 $\pm$ 0.05 and 0.6 $\pm$ 0.05, respectively (Figure 3.3). Squirreltail (*Elymus elymoides* (Raf.) Swezey) was the most common LNPB, occurring on 35% of the sites. Cheatgrass (*Bromus tectorum* L.), the most common annual grass, was found on 88% of sites. Longleaf phlox (*Phlox longifolia* Nutt.) was the most common perennial forb (46% of the sites) and burr buttercup (*Ceratocephala testiculata* (Crantz) Roth) and slender phlox (*Microsteris gracilis* (Hook.) Greene) were the most common annual forbs (64% of the sites, each). Wyoming big sagebrush was the most common shrub and occurred on 63% of the sites. Large native perennial bunchgrasses and Wyoming big sagebrush occurred together on 49% of the sites and LNPB, sagebrush and perennial forbs occurred together on 39% of the sites.

Basal cover varied widely among and within herbaceous functional groups (Figure 3.4). Fifty percent of the sites contained at least 2.4% Sandberg bluegrass basal cover which ranged from 0 to 13%. Basal cover of LNPB ranged from 0 to 10% although 41% of the sites had no LNPB basal cover and 50% of the sites contained less than 1% LNPB basal cover. Basal cover of crested wheatgrass was over 5% on 50% of the sites and ranged from less than 1% to 19%. Shrubs canopy cover ranged from 0 to 27% and 50% of the sites had at least 3.4% cover. Eighteen (15%) of the sites had sagebrush cover greater than 10%. Moss and crypto-biotic crust cover ranged from 0 to 13%. Fifty percent of sites contained over 3% moss cover but only 32% of the sites had more than 1% crypto-biotic crust cover.

Density varied widely among and within herbaceous functional groups (Figure 3.5). Density of Sandberg bluegrass ranged from 0 to 119 plants·m^{-2} and 50% of the sites contained at least 17.4 Sandberg bluegrass plants·m^{-2}. Forty-three percent of sites contained no LNPB individuals. Of the sites containing LNPG, 55% had less than 1 LNPB plant·m^{-2} and 45% had LNPB densities between 1 and 10 plants·m^{-2}. Density of shrubs ranged from 0 to 2 plants·m^{-2}. Fifty percent of sites had at least 0.4 shrubs·m^{2} and 12% of sites contained no shrubs. Density of crested wheatgrass ranged from 0.25 to 22 plants·m^{-2} and half of the sites had more than 7.6 crested wheatgrass plants·m^{-2}. Density of annual forbs ranged from 0 to 769 plants·m^{-2} and 50% of the sites contained at least

29.3 annual forb plants·m^{-2}. Density of annual grasses ranged from 0 to 757 plants·m^{-2} and 50% of the sites contained at least 11.8 annual grass plants·m^{-2}.

3.4.1 Functional group correlations

There was no correlation between crested wheatgrass cover or density and species richness or species diversity (adj. $R^2 < 0.10$, $p > 0.05$). Crested wheatgrass density was not correlated with the density of any functional group (adj. $R^2 < 0.10$, $p > 0.05$). Crested wheatgrass basal cover was not correlated with the basal cover of any herbaceous functional group (adj. $R^2 < 0.10$, $p > 0.05$). Foliar cover of shrubs was slightly negatively correlated with basal cover of crested wheatgrass (adj. $R^2 = 0.26$, $p < 0.001$). Wyoming big sagebrush foliar cover was slightly negatively correlated with crested wheatgrass cover (adj. $R^2 = 0.24$, $p < 0.001$).

Sandberg bluegrass density was positively correlated with large native perennial bunchgrass density (adj. $R^2 = 0.90$, $p < 0.001$). LNPB density was positively correlated with perennial forb density (adj. $R^2 = 0.29$, $p < 0.001$).

Annual grass density was positively correlated with litter cover (adj. $R^2 = 0.45$, $p < 0.001$). Litter cover was negatively correlated with cover of bare ground (adj. $R^2 = 0.49$, $p < 0.001$)

3.4.2 Multiple linear regression

Sandberg bluegrass cover and density were positively correlated with a higher percentage of silt in the soil and more eastern longitudes (Table 3.2 & 3.3). Sandberg bluegrass basal cover was positively correlated with elevation (Table 3.2). Higher basal cover of crested wheatgrass was correlated with greater carbon concentrations, a higher C:N ratio in the soil and more basic soils. Basal cover of crested wheatgrass was negatively correlated with silt and gravel cover (Table 3.2). Crested wheatgrass density was weakly correlated measured environmental variables (adj $R^2 = 0.11$, $p < 0.05$; Table 3.2). Large native perennial bunchgrasses density was positively correlated with increased soil silt, less basic soil pH and more eastern sites ($R^2 = 0.56$ respectively; Table 3.3). Large native perennial bunchgrasses basal cover was weakly correlated with measured environmental variables (adj $R^2 = 0.19$, $p < 0.05$; Table 3.3). Perennial forb cover and density were negatively correlated with percent sand in the soil and more acidic soils (Table 3.2 & 3.3). Perennial forb cover was positively correlated with higher soil carbon and higher gravel cover (Table 3.2) and perennial forb density was positively correlated with higher rock cover (Table 3.3). Annual forb cover was positively correlated with clay content and average annual precipitation and negatively correlated with gravel cover (Table 3.2). Annual forb density was not significantly correlated with any measured environmental variables (adj $R^2 < 0.10$, $p > 0.05$). Shrub cover and density were negatively correlated with sandiness and average annual precipitation and positively correlated with elevation (Table 3.2 & 3.3). Shrub density was higher in neutral to slightly acidic soil (Table 3.3). Wyoming big sagebrush foliar cover and density were weakly correlated with environmental variables (adj $R^2 = 0.22$ and 0.18, $p < 0.001$; Table 3.2 & 3.3). Sagebrush cover was positively correlated with gravel cover and negatively correlated with sandy soil, soil pH and average annual precipitation (Table 3.2).

Total species richness was associated with lower soil carbon, higher soil nitrogen and a lower C:N ratio (Table 3.4). Perennial herbaceous species richness was positively correlated with soil carbon (Table 3.5). Perennial herbaceous species diversity was associated with lower soil carbon and a lower C:N ratio (Table 3.5). Richness and diversity were positively correlated with more neutral to slightly acidic soils (Table 3.4 & 3.5). Herbaceous perennial and total species richness and total species diversity were negatively correlated with increasing sand and perennial herbaceous diversity was positively correlated with higher clay content. Richness and diversity were positively correlated with rock cover (Table 3.4 & 3.5). Total species diversity was positively correlated with higher elevations and perennial herbaceous species diversity was positively correlated with sites with a higher heat load index.

3.4.3 Ground Cover Correlations

Litter cover and crypto-biotic crust cover were positively correlated with sandy soil (Table 3.6). Bare ground was positively correlated with more clayey soil. Litter was positively and bare ground was negatively correlated with soil nitrogen. Crypto-biotic crusts were positively correlated with higher C:N ratios (Table 3.6). Bare ground and litter were negatively correlated with gravel but crypto-biotic crust cover was positively correlated with gravel. Bare ground was negatively correlated with rockiness. Litter was positively and bare ground was negatively correlated with longitude (Table 3.6). Moss was not significantly correlated with any measured environmental variables ($R^2 < 0.20$; $p > 0.05$).

3.5 DISCUSSION

Vegetation composition of crested wheatgrass stands was quite variable. Though near-monocultures of crested wheatgrass existed, some stands had relatively abundant native vegetation, especially shrubs (Figure 3.1). Correlations between environmental variables and vegetation characteristics suggest that, at times, large amounts of the variability in the cover and abundance of native vegetation in crested wheatgrass stands is likely related to environmental differences (Table 3.2 & 3.3). This may be part of the reason that some authors (Looman and Heinrichs 1973; Marlette and Anderson 1986) have reported that seeding crested wheatgrass results in near monocultures of crested wheatgrass and others have found more diverse assemblages (Reynolds and Trost 1981; McAdoo et al. 1989). The correlation between environmental factors and native vegetation may be useful to identify where native vegetation is more likely to co-exist with crested wheatgrass and where crested wheatgrass is likely to form monocultures.

The amount of variation of different herbaceous functional groups explained by measured environmental characteristics was quite variable. At the low end, environmental factors were not correlated with the variability in annual grass density compared to 56% of the variability of LNPB density (Table 3.3). Perennial forb basal cover and density and Sandberg bluegrass basal cover and density variability were also fairly well explained by environmental factors (R^2 = 0.44 – 0.49). Though a variety of environmental factors were included in regression models, soil texture appeared to be the most consistently included factor. Soil texture was included in the best regression models for cover and density of all plant functional groups. Other studies in the Great Basin have also suggested that soil texture might be one of the most important variables predicting herbaceous composition (Raven 2004; Davies et al. 2007a; Williams 2009). Soil texture may be important because it affects moisture availability; sandier soil has a lower water holding capacity and retains less water in the root zone than finer textured soil (Shown et al. 1969). Crested wheatgrass takes up soil moisture and nutrients more quickly than native bunchgrass species and, therefore, may be better able to take advantage of limited moisture in sandier soils than many native herbaceous species (Eissenstat and Caldwell 1988). In addition, intact Wyoming big sagebrush sites with sandy soils generally have less native herbaceous vegetation and less sagebrush cover than sites with more fine textured soils (Davies et al. 2006; Davies et al. 2007a). Therefore, some of this effect may be inherent regardless of whether or not crested wheatgrass was seeded on these sites. It is also possible that initial seeding success of crested wheatgrass plantings was higher on sandier soils and Wyoming big sagebrush reestablishment was more rapid on more fine textured soil (Shown et al. 1969).

Perennial herbaceous species richness and diversity was lower on our sites than in relatively intact Wyoming big sagebrush communities across eastern Oregon. The average perennial herbaceous species richness and diversity in intact Wyoming big sagebrush communities were 14.4 species and 1.6, respectively (Davies and Bates 2010b). This was about three times as high as the average richness (5.5) and diversity (0.6) we found on sites seeded to crested wheatgrass. Krzic et al. (2000) also found reduced species diversity in fields seeded with crested wheatgrass than on nearby native vegetation sites. However, this study was not designed to test the effects of seeding crested wheatgrass on community richness and diversity as we did not compare seedings to unseeded communities. Although our results suggest a relationship, we cannot attribute the lower richness and diversity to crested wheatgrass. The low richness and diversity in our study sites may be an artifact of plant community composition at the time of seeding since many seedings were implemented following a disturbance that reduced native vegetation.

Some locations may also be more inclined to have native vegetation as we found that richness and diversity generally increased as soil texture became less coarse. Similar to our results, soil texture was an important factor associated with species richness and diversity of Rocky Mountain grasslands with greater richness associated with higher silt content in the soil (Stohlgren et al. 1999). This indicates that water and nutrient availability associated with soil texture may be an important factor explaining variability in richness and diversity.

Richness and species diversity on our sites were positively correlated with rockiness (Table 3.4; 3.5). It is possible that rocks create microhabitats and therefore multiple niches (Milchunas and Noy-Meir 2002; Lambrinos et al. 2006). Rocks may also convey protection from herbivores, creating safe sites for more grazing sensitive native species or by catching seeds to recolonize overgrazed microsites (Milchunas and Noy-Meir 2002; Golodets et al. 2011). Rocks can also affect soil hydrology as water can accumulate on the underside of surface and subsurface rocks to provide a more persistent water source (Hamerlynck et al. 2002). Although Williams (2009) suggested that rockiness may play a role in the likelihood of a site being successfully seeded to crested wheatgrass, site rockiness did not explain any of the variation in crested wheatgrass cover or density across the 121 sites sampled in our study.

Large native perennial bunchgrasses were the least likely functional group to occur in the crested wheatgrass communities we sampled across southeastern Oregon. This may be because LNPB are likely to have been negatively impacted by overgrazing (Caldwell et al. 1981; Mack and Thompson 1982; Brewer et al. 2007) prior to seeding crested wheatgrass and are generally less competitive than crested wheatgrass (Bakker and Wilson 2001). We were, in most cases, unable to determine pre-seeding plant community composition at sampled sites, but speculate that many may have been overgrazed for decades prior to seeding crested wheatgrass. Large native perennial bunchgrasses were likely not only depleted in the community prior to seeding of crested wheatgrass, but subsequently had limited re-establishment due to crested wheatgrass competition (Heady 1988; Pyke 1990; Fansler and Mangold 2011). Although 10% of our sampled sites had a higher density of native perennial bunchgrasses than crested wheatgrass, we found, overall, few LNPB in most stands of crested wheatgrass. Native perennial bunchgrasses do not generally increase on sites when seeded in conjunction with non-native perennial grass species such as crested wheatgrass (Knutson et al. 2014; Nafus et al. 2015) and are frequently outcompeted by crested wheatgrass (Bakker and Wilson 2001). Large native perennial bunchgrasses can be difficult to establish in crested wheatgrass dominated plant communities, even with management to reduce crested wheatgrass (Hulet et al. 2010; Fansler and Mangold 2011).

Perennial forbs were less common on sandy soil. Sandy soil was similarly associated with lower perennial forb cover in intact Wyoming big sagebrush communities (Davies et al. 2006), possibly because competition may be exacerbated on sandy soils which have lower soil water and nutrient availability (Binkley and Vitousek 1989). Crested wheatgrass may limit perennial forbs as it can be highly competitive with forb species and has been used to prevent reinvasion by exotic forb species in Montana (Sheley and Carpinelli 2005). However, effects of crested wheatgrass on native perennial forbs in the Great Basin are relatively unknown. Density and diversity of forbs appear to be lower in crested wheatgrass seedings as we found lower density and diversity of perennial forb species than Davies and Bates (2010a, b) found in intact Wyoming big sagebrush plant communities in southeastern Oregon.

Annual forbs, annual grasses, and Sandberg bluegrass, the three most prevalent herbaceous functional groups in stands of crested wheatgrass, tend to avoid resource limitations by growing earlier in the season than crested wheatgrass, when resources are more plentiful (Ludlow 1989; Volaire et al. 2009). The ability to temporally avoid competition for resources may explain their success in crested wheatgrass stands relative to plant functional groups that are more likely to have to compete with crested wheatgrass when resources are limited (e.g. large native perennial bunchgrasses). In addition, these functional groups are often found to increase as a result of overgrazing (Hubbard 1951), which likely preceded the planting of crested wheatgrass in many seedings. Therefore, it is probable that these early growing species were abundant on some of these sites prior to seeding (Heady 1988).

Wyoming big sagebrush constituted the majority of the shrub cover (74%) and density (62%). Similarly to (Davies et al. 2007a), we did not find strong correlations between Wyoming big sagebrush density or cover and any of measured environmental characteristics. Our data does suggest that, in agreement with Davies et al. (2006; 2007a) and in contrast to Williams (2009), Wyoming big sagebrush was negatively correlated with more sandy soils. Plant communities with higher numbers of shrubs, most of which were Wyoming big sagebrush, tended to be associated with soils higher in silt and lower in precipitation. It is possible that in our case, shrubs tended to dominate sites with less precipitation because shrubs were able to access moisture deeper in the soil profile that was less accessible to herbaceous vegetation giving shrubs a competitive advantage on these sites (Jensen et al. 1990; Dodd et al. 2002). Alternatively, sites with lower precipitation may have had lower initial crested wheatgrass establishment, and therefore lower crested wheatgrass competition allowing sagebrush to more rapidly recover following pre-seeding treatments (Shown et al. 1969). However, associations were relatively weak as only 22% of the variation in Wyoming big sagebrush cover was explained by environmental variables. Therefore, precipitation and soil texture may not have much effect on the likelihood of sagebrush reestablishment into crested wheatgrass seedings. Similarly, Rittenhouse and Sneva (1976) found that crested wheatgrass cover declined with increasing cover of Wyoming big sagebrush.

Though we could only explain a small portion of the variability in Wyoming big sagebrush density and cover, it occurred on 63% of the seedings. Because many sites were seeded after fire (which removes sagebrush) or intentional sagebrush removal, this suggests sagebrush was recruited into these communities. Wyoming big sagebrush recovery after disturbance can be slow, often taking several decades to a century (Watts and Wambolt 1996; Baker 2006; Boyd and Svejcar 2011). Thus, having 15% of the crested wheatgrass seedings with 10% or higher sagebrush cover suggests that, in some cases, sagebrush recovery can occur to levels sufficient to provide habitat for sagebrush-associated wildlife species. At 10% sagebrush cover these seedings meet guidelines for minimum sagebrush cover winter habitat for greater sage-grouse (*Centrocercus urophasianus*) (McAdoo et al. 1989; Connelly et al. 2000). Relatively intact Wyoming big sagebrush plant communities had an average density of mature sagebrush around 0.5 individuals·m^{-2} (Davies and Bates 2010b). On our sites Wyoming big sagebrush density averaged 0.2 individuals·m^{-2} although some sites had over 1 individual·m^{-2}.

Most communities seeded to crested wheatgrass were degraded, burned in a wildfire and/or treated in an attempt to remove shrub species prior to seeding (Heady 1988), thus native vegetation cover and abundance at some sites may have been an artifact of plant community composition prior to seeding. The type and severity of disturbance as well as plant composition prior to seeding is likely to have affected current plant composition (Burke and Grime 1996). Unfortunately, data on the plant community prior to seeding was not available for most of the sites sampled. Fire, time since seeding, grazing and other management actions may also affect composition. Regrettably, historical management and disturbance information was incomplete for the 121 sites sampled. Our data was collected across sites with variable management history, and this suggests that there are some environmental factors that influence plant community composition of crested wheatgrass seedings regardless of management and initial floristics. Our results also suggest that the effects of seeding crested wheatgrass vary considerably by site characteristics and that native vegetation can co-occupy some rangelands seeded with crested wheatgrass. This information may be useful for prioritizing where restoration of sagebrush communities seeded with crested wheatgrass should be applied and assessing the potential effects of seeding crested wheatgrass. For instance, native vegetation is more likely to coexist with crested wheatgrass on less coarse-textured soils.

3.6 FIGURES

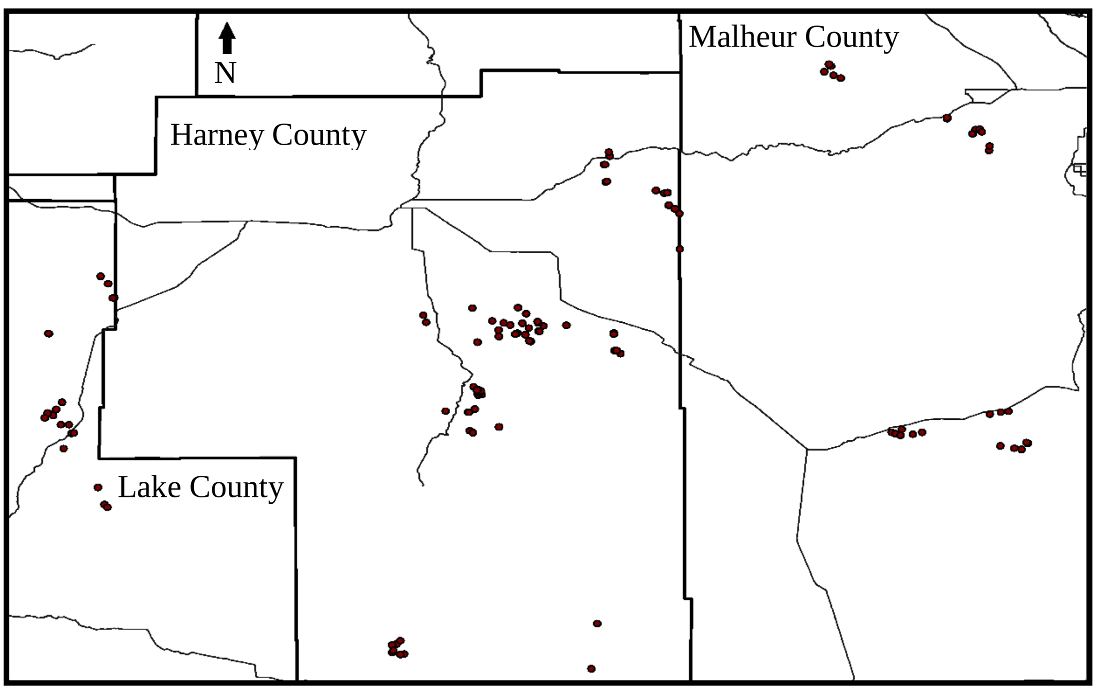

Figure 3.1. Locations of sites across southeastern Oregon. Red circles represent areas where crested wheatgrass seedings were sampled.

Figure 3.2. A near monoculture crested wheatgrass seeding (left) and a Wyoming big sagebrush dominated crested wheatgrass seeding (right).

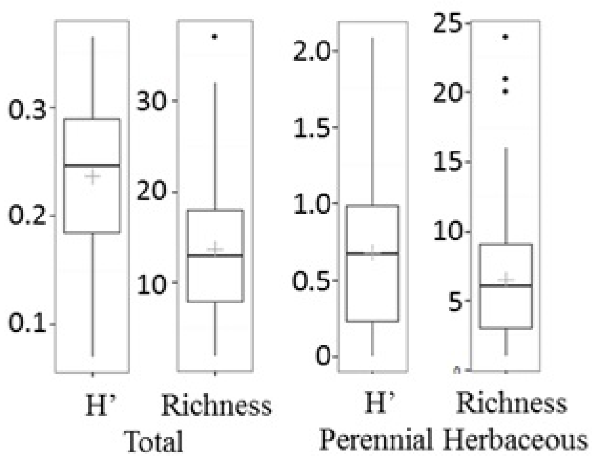

Figure 3.3. Boxplot showing total and perennial herbaceous Shannon-Weiner Diversity (H') and species richness across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the solid black line, the mean is depicted as a grey cross. The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 * the inter-quartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

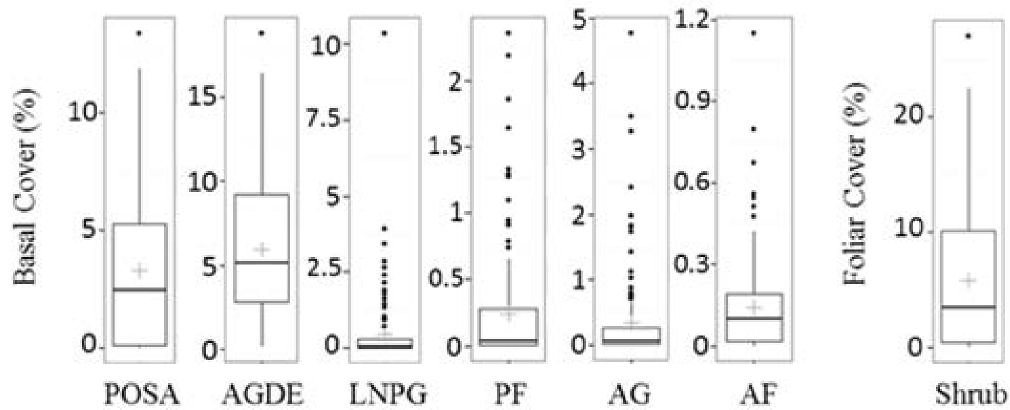

Figure 3.4. Boxplot showing the percent basal cover of Sandberg bluegrass (POSA), crested wheatgrass (AGDE), large native perennial bunchgrass (LNPB), perennial forbs (PF), annual grass (AG), and annual forbs (AF) and foliar cover (%) of shrubs across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the solid black line, the mean is depicted as a grey cross. The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 * the inter-quartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

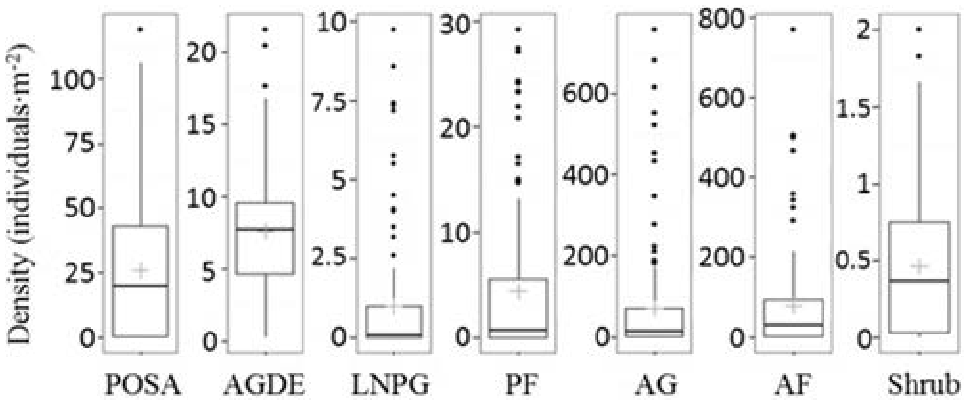

Figure 3.5. Boxplot showing density (plants·m^{-2}) of Sandberg bluegrass (POSA), crested wheatgrass (AGDE), large native perennial bunchgrass (LNPB), perennial forbs (PF), annual grass (AG), annual forbs (AF) and shrubs across 121 crested wheatgrass stands sampled in southeastern Oregon. The median is shown as the solid black line, the mean is depicted as a grey cross. The upper and lower ends of the box correspond to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the 25th and 75th percentiles to the lowest or highest value that is within 1.5 * the inter-quartile range. Data beyond the end of the whiskers are outliers and plotted as points (as specified by Tukey).

3.7 TABLES

Table 3.1. Environmental factors and vegetation characteristics measured at or calculated for each of 121 sites located in crested wheatgrass seedings across a 54230 km^2 area in southeastern Oregon.

Vegetation characteristics	Environmental factors	Calculated parameters
Herbaceous basal cover	Longitude and latitude	Vegetation
Herbaceous density	Slope	Shannon Weiner Diversity (H')
Shrub foliar cover	Elevation	Species Richness
Shrub density	Aspect	
	Soil texture 0 – 15 cm	Environmental
Ground cover	(% Sand, Silt and Clay)	Heat load index
characteristics	Soil texture 16 - 60 cm	
Moss	(% Sand, Silt and Clay)	
Crypto-biotic crust	Soil total carbon and nitrogen (0-15 cm) (%)	
Bare ground	Carbon:nitrogen ratio	
Litter	Soil pH (0-15 cm)	
	Average annual precipitation (30 year)	
	Average max temperature (April-September)	
	Average min temperature (October-March)	
	Rock (% cover)	
	Gravel (% cover)	

* Soil texture (15-60 cm) was originally included in the analysis but because of missing values in the data and a 99% correlation with the 0-15 cm values, it was removed from the analysis.

Table 3.2. Multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPB), annual grass, perennial forb, and annual forb basal cover and shrub and Wyoming big sagebrush (ArtrWy) foliar cover. Direction of association (+ or -), correlation estimates and (SE) are shown for environmental variables selected using mixed model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only functional groups that had an adjusted $R^2 > 0.10$ were included in the table. All coefficients of variation (R^2) were significant at $p < 0.05$.

Functional Group Basal Cover (%)	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover (%))	Sqrt (Rock cover (%))	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Sandberg bluegrass	0.46	+ 219.13 (41.89)	+ 0.10 (0.018)									+ 1.89 (0.36)	+ $4.2e^{-3}$ ($1.4e^{-3}$)	
Crested wheatgrass	0.30	– 12.33 (6.51)	– 0.10 (0.023)				+ 34.00 (7.96)	+ 0.81 (0.20)	+ 1.89 (0.78)	– 0.86 (0.22)				
Sqrt (LNPB)	0.19	+ 2.37 (0.70)		– $7.0e^{-3}$ ($2.7e^{-3}$)					– 0.28 (0.11)	+ 0.11 (0.032)				
Sqrt (Annual grass)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sqrt (Perennial forb)	0.44	+ 2.73 (0.45)		– $5.8e^{-3}$ ($1.6e^{-3}$)			+ 1.66 (0.71)		– 0.35 (0.065)	+ 0.40 (0.019)				
Sqrt (Annual forbs)	0.20	– 0.067 0.15			+ $8.0e^{-3}$ ($2.0e^{-3}$)					– 0.039 (0.013)				+ $1.1e^{-3}$ ($5.4e^{-4}$)
Sqrt (Shrubs)	0.20	11.15 (3.20)		– 0.022 ($1.4e^{-3}$)									+ $2.3e^{-3}$ ($6.7e^{-4}$)	– 0.017 ($4.2e^{-3}$)
Sqrt (ArtrWy)	0.22	+ 14.2 (3.18)		– 0.017 ($7.2e^{-3}$)					– 1.40 (0.34)	+ 0.19 (0.090)				– 0.011 ($4.4e^{-3}$)

Table 3.3. Multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPB), annual grass, perennial forb, annual forb, shrub and Wyoming big sagebrush (ArtrWy) abundance (plants·m^{-2}). Direction of association (+, -), correlation estimates and (SE) are shown for environmental variables selected using mixed model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only functional groups that had an adjusted $R^2 > 0.10$ were included in the table. All coefficients of variation (R^2) were significant at $p < 0.05$.

Functional Group Density (plants·m^{-2})	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover (%))	Sqrt (Rock cover (%))	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Sandberg bluegrass	0.49	+ 1291.38 (278.75)	+ 0.92 (0.14)									+ 10.94 (2.33)		
Crested wheatgrass	0.11	+ 7.06 (1.10)	– 0.060 (0.027)			+ 3.31 (0.88)								
Sqrt (LNPB)	0.56	+ 142.62 (29.80)	+ 0.11 (0.015)						– 1.34 (0.45)			+ 1.12 (0.25)		
Sqrt (Annual grass)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sqrt (Perennial forb)	0.45	+ 12.56 (1.66)		– 0.039 ($6.2e^{-3}$)					– 1.44 (0.26)		+ 0.19 (0.098)			
Sqrt (Annual forbs)	0.14	+ 232.98 (72.80)			+ 0.16 (0.055)							+ 1.94 (0.61)	+ 0.010 ($4.7e^{-3}$)	
Sqrt (Shrubs)	0.20	+ 3.04 (0.87)		– $4.9e^{-3}$ ($2.0e^{-3}$)					– 0.30 (0.093)				+ $6.0e^{-4}$ ($1.8e^{-4}$)	– $3.9e^{-3}$ ($1.1e^{-3}$)
Sqrt (ArtrWy)	0.18	+ 3.34 (0.79)		– $4.5e^{-3}$ ($1.8e^{-3}$)					– 0.33 (0.087)	+ 0.047 (0.022)				– $2.3e^{-3}$ ($1.1e^{-3}$)

Table 3.4. Multiple linear regression models for total species richness and total Shannon-Weiner Diversity (H') Direction of association (+,-), correlation estimates and (SE) are shown for environmental variables selected using mixed model selection. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. All coefficients of variation (R^2) were significant at $p < 0.05$.

All species	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover (%))	Sqrt (Rock cover (%))	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Richness	0.50	+ 77.89 (10.69)		– 0.071 (0.031)		+ 14.44 (3.97)	– 76.96 (33.57)	– 2.29 (0.65)	– 6.58 (1.35)		+ 1.91 (0.48)			
Diversity	0.37	+ 3.91 (0.82)		– 0.011 ($2.5e^{-3}$)					– 0.48 (0.11)		+ 0.10 (0.038)		+ $5.8e^{-4}$ ($2.3e^{-4}$)	

Table 3.5. Multiple linear regression models for perennial herbaceous species richness and perennial herbaceous Shannon-Weiner Diversity (H'). Direction of association(+,-), correlation estimates and (SE) are shown for environmental variables selected using mixed model selection. table. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. All coefficients of variation (R^2) were significant at $p < 0.05$.

Perennial herbaceous species	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover (%))	Sqrt (Rock cover (%))	Longitude (decimal degrees)	Elevation (m)	Heat Load Index
Richness	0.45	+ 34.42 (5.52)		– 0.061 (0.019)			+ 28.86 (8.36)		– 4.32 (0.81)		+ 0.90 (0.30)			
Diversity	0.48	+ 1.17 (1.47)			+ 0.016 ($4.0e^{-3}$)	+ 1.23 (0.26)	– 7.41 (2.25)	– 0.19 (0.042)	– 0.30 (0.090)		+ 0.082 (0.032)			+ 2.73 (1.33)

Table 3.6. Multiple linear regression models for ground cover. Direction of association (+,-), correlation estimates and (SE) are shown for environmental variables selected using mixed model selection. Only ground cover groups that had an adjusted $R^2 > 0.10$ were included in the table. Variables were square root transformed (Sqrt) or natural log (ln) when necessary to meet model assumptions. All coefficients of variation (R^2) were significant at $p < 0.05$.

Ground Cover (%)	Adj R^2	Intercept	Silt (%)	Sand (%)	Clay (%)	Nitrogen (%)	Carbon (%)	C:N ratio	pH	Sqrt (Gravel cover (%))	Sqrt (Rock cover (%))	Longitude (decimal degrees)	Elevation (m)	Precipitation (mm)
Liter	0.22	+ 522.12 (156.91)		+ 0.17 (0.062)		+ 10.44 (2.32)				– 1.55 (0.71)		+ 4.24 (1.34)		
Bare ground	0.37	– 761.81 (157.62)			+ 0.045 (0.11)	– 14.07 (2.37)				– 3.71 (0.77)	– 3.66 (0.90)	– 6.92 (1.33)		
Moss	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ln (Crtpto-biotic crust)	0.27	– 14.24 (2.03)	+ 0.11 (0.025)	+ 0.071 (0.020)				+ 0.56 (0.12)		+ 0.27 (0.13)				

4 Prior disturbance history, management, and seeding year precipitation associations with vegetation characteristics of crested wheatgrass stands

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Prepared for submission to Environmental Management

4.1 ABSTRACT

Crested wheatgrass has been seeded across millions of hectares of the Great Basin sagebrush steppe and is often associated with native species displacement and low biological diversity; however, composition of these seedings can be quite variable. To gain better understanding of the correlation between the vegetation composition in crested wheatgrass seedings and their seeding history and livestock management, we evaluated crested wheatgrass seedings across a 54230 km^2 area in southeastern Oregon. We found that higher precipitation in the year following a crested wheatgrass seeding has long-term, negative effects on Wyoming big sagebrush cover and density. Wyoming big sagebrush cover and density were positively correlated with age of seeding and time since fire. Though native vegetation was generally negatively associated with increasing stocking rate ($AUMs \cdot ha^{-1}$), we postulate that was largely the effect of more AUMs being allotted to more successful crested wheatgrass seedings. Further supporting this hypothesis, sites that were grazed contained more native herbaceous vegetation and shrubs than ungrazed sites. We also found that pre-seeding treatment/disturbance (burned, scarified, plowed, or herbicide) appears to have long-term implications for plant community dynamics. The results of this study suggest that a number of factors influence native vegetation presence within stands of seeded crested wheatgrass. Pre-seeding disturbance treatments and precipitation in the year following the seeding have long-term legacy effects on community composition characteristics. Crested wheatgrass seedings that experience livestock grazing were associated with higher native vegetation cover and density than are ungrazed seedings. This suggests that management actions can be used to

affect the cover and abundance of native vegetation in crested wheatgrass stands and that moderate grazing can be used to reduce monoculture characteristics of crested wheatgrass seedings.

4.2 INTRODUCTION

Crested wheatgrass (*Agropyron cristatum* [L] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.), an introduced perennial bunchgrass, has been seeded across 6 – 11 million hectares of western North American rangelands (Lesica and DeLuca 1996; Ambrose and Wilson 2003; Hansen and Wilson 2006). Crested wheatgrass was originally seeded in sagebrush (*Artemisia* L.) communities to increase livestock forage and reduce halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey), a plant that is toxic to sheep (Miller 1943; Miller 1956; Frischknecht and Harris 1968; Vale 1974). Seeding of crested wheatgrass into sagebrush habitat following wildfires continues into present day because of its ability to suppress undesirable annual grasses (Arredondo et al. 1998; Davies et al. 2010b), its relative low cost and ease of establishment compared to native species (Pellant and Lysne 2005; Boyd and Davies 2010; James et al. 2012; Davies et al. 2015), and to reduce erosion and increase livestock forage (Dormaar and Smoliak 1985; Smoliak and Dormaar 1985; Dormaar et al. 1995).

Although crested wheatgrass has many desirable competitive benefits against undesirable weed species, its strong competitiveness can allow it to form near monocultures with significantly reduced cover and richness of native vegetation species and reduced wildlife habitat (Looman and Heinrichs 1973; Christian and Wilson 1999; Heidinga and Wilson 2002). As we found in chapter 3, some crested wheatgrass seedings remain a near monoculture for decades (Hull and Klomp 1966; Looman and Heinrichs 1973; Marlette and Anderson 1986) while others have a higher native vegetation component, particularly shrubs (Reynolds and Trost 1981; McAdoo et al. 1989). Native vegetation cover and abundance within a crested wheatgrass seeding can be highly variable (see Hull and Klomp 1966; Looman and Heinrichs 1973; Reynolds and Trost 1981; Marlette and Anderson 1986; McAdoo et al. 1989; Krzic et al. 2000). As vegetation diversity in a crested wheatgrass seeding increases, so does wildlife habitat and wildlife diversity (Vale 1974; Reynolds and Trost 1981; Parmenter and MacMahon 1983; McAdoo et al. 1989). However, it is not clear why some crested wheatgrass seedings remain near monocultures and others have more abundant native vegetation. Although some of the variation in native vegetation cover and diversity in crested wheatgrass seedings can be explained by edaphic factors (Raven 2004; Williams 2009), it is not known how past and present management activities influence native vegetation characteristics in crested wheatgrass seedings.

Precipitation at the time of seeding along with pre-seeding disturbances, including mechanical, burning and herbicide treatments, and post-seeding disturbances, including fire and livestock grazing practices (intensity, duration, season and animal type), can influence plant community dynamics of sagebrush ecosystems (Hull and Klomp 1967; Shown et al. 1969; Cox and Anderson 2004; Strand et al. 2014). Historically, fire, herbicide and mechanical treatments such as plowing, chaining, and disking were often used on a site prior to seeding to prepare the soil and reduce residual vegetation (Vale 1974). Pre-seeding disturbance method, in combination with seeding year precipitation, can influence the initial recovery of native vegetation species, particularly sagebrush, and seeded crested wheatgrass germination and establishment (Hull and Klomp 1967; Cluff et al. 1983; Cox and Anderson 2004) which, in turn, likely affects long-term community plant dynamics. On Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) sites where crested wheatgrass was not seeded, sagebrush control method influences long-term recovery of sagebrush (Wambolt and Payne 1986; Watts and Wambolt 1996). On sites seeded with crested wheatgrass, however, there is a lack of information about the long-term differences in native vegetation cover and abundance associated with different methods of pre-seeding sagebrush control.

Following seeding, livestock management and disturbance frequency can impact plant community dynamics. Although crested wheatgrass is very tolerant of grazing and can withstand heavy grazing for many years (Cook et al. 1958; Hull and Klomp 1966; Hull 1974; Caldwell et al. 1981; Laycock and Conrad 1981), heavy grazing may facilitate the reintroduction of more grazing tolerant native bunchgrasses such as Sandberg bluegrass (*Poa secunda* J. Presl) (Hyder and Sawyer 1951). Heavy spring grazing may be associated with increased shrub cover and reduced crested wheatgrass dominance (Laycock 1967) whereas, moderate grazing in native Wyoming big sagebrush ecosystems does not generally appear to alter shrub cover (Rice and Westoby 1978; Courtois et al. 2004; Yeo 2005; Davies et al. 2010a; Strand et al. 2014), although moderate levels of season-long and summer grazing may increase Wyoming big sagebrush cover (Angell 1997).

Wyoming big sagebrush and perennial bunchgrass species are not as well adapted to fire as crested wheatgrass. Sagebrush is readily killed by fire and can take up to 30 or more years to recover (Wambolt and Payne 1986; Skinner and Wakimoto 1989). Burning sagebrush frequently results in 100% mortality although some individuals may survive and provide a potential seed source for eventual re-establishment (Cluff et al. 1983; Wambolt and Payne 1986; Wambolt et al. 2001; Ziegenhagen and Miller 2009). Crested wheatgrass burns quickly with little heat transfer into the soil and is therefore more resilient to fire than many native bunchgrass species (DePuit 1986; Skinner and Wakimoto 1989). Following fire, crested wheatgrass can quickly take advantage of reduced sagebrush competition and can increase by 3-6 fold three years post-fire (Ralphs and Busby 1979). Although spring burning can decrease crested wheatgrass production for several years, post-fire recovery of crested wheatgrass is generally rapid, especially if fire occurs in the late summer or fall (Young 1983; Bradley et al. 1992). This possibly suggests that wildfire in a crested wheatgrass seeding enables crested wheatgrass to maintain a near-monoculture status.

Abiotic factors such as elevation, precipitation and soil texture help explain some of the variability in native vegetation presence (Raven 2004; Williams 2009; Nafus et al. Chapter 3); however, there is a lack of understanding about the influence of disturbance events such as fire and livestock use on the community characteristics of crested wheatgrass seedings (Grant-Hoffman et al. 2012). Crested wheatgrass has been extensively seeded across millions of acres of historic sage grouse habitat and it is, therefore, critical to understand the factors that might be associated with higher presence of native vegetation (Knick et al. 2003; Schroeder et al. 2004; Pellant and Lysne 2005; Davies et al. 2011).

We predicted that increased grazing pressure (as estimated by average AUMs·ha^{-1} and distance to water [m]) on spring grazed pastures would be positively associated with higher shrub cover and abundance. We expected sites that were seeded or burned more recently to have lower native vegetation density and cover. We also expected sites that were burned prior to seeding to have lower Wyoming big sagebrush cover and density than sites that had been treated with herbicides, scarified or plowed.

4.3 METHODS

4.3.1 Study area description

Study sites were selected across a 54230 km^2 area in southeastern Oregon. Study locations were generally in Wyoming big sagebrush-bunchgrass ecological sites though a few locations were more alkaline and had been characterized by shrubs such as spiny hopsage (*Grayia spinosa* (Hook.) Moq.) and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). All study locations were seeded with crested wheatgrass 10 to 50 years prior using largely drill seeding methods. Seeding method was rarely included in seeding records and, of the sites with records on seeding method, 95% were drill seeded. Therefore, seeding method was not included as an explanatory variable. Long-term annual precipitation for study locations averaged between 200 and 360 mm (PRISM). Annual precipitation amounts (from 1 October to 30 September) for study locations were 74% of the long-term average (30 years) in 2011-2012 and 75% of the long-term average in 2012-2013. Precipitation in the study area arrives mainly as snow from November to March and as rain from April to May and summers are typically hot and dry. Topography and soils were variable across the study area. Elevation of sites ranged from 819 m to 1739 m.

4.3.2 Site selection

Expert personnel from the U.S. Department of Interior Bureau of Land Management (BLM) of the Burns, Lakeview, and Vale BLM Districts, Fish and Wildlife Service (USFWS), and the Oregon Department of State Lands (ODSL) were consulted to obtain the locations of all crested wheatgrass seedings in their jurisdiction. One hundred and twenty one sites were located and then measured in June-August 2012 and 2013. Sites were sampled across a gradient of environmental conditions to capture a range of crested wheatgrass dominance and variability of native vegetation. All sites sampled had been identified as having been seeded with crested wheatgrass and contained at least 0.25 crested wheatgrass plants per m^2 to ensure that they had been successfully seeded.

4.3.3 Vegetation characteristics

Vegetation characteristics were measured using the methods described in Chapter 3, section 3.3.3.

4.3.4 Management factors

We used information provided by the management personnel who assisted with seeding selection in conjunction with GIS maps available online (USDI-BLM 2014) in Arc Map 10.0 (ESRI (Environmental Systems Resource Institute) 2011) to determine grazing, seeding and fire history for the sites whenever the information was available. Ninety-one sites had seeding year and fire history information. Sixty-three of these sites had information about pre-seeding disturbance. Four types of pre-seeding disturbance occurred: fire (31 sites), plowing (8 sites), herbicide (9 sites) and soil scarification (15 sites). Soil scarification involved using chains or harrows to increase bare mineral soil and improve seed-soil contact. Type of herbicide used was not always included in the seeding record but was typically aerially applied 2,4-D, especially on seedings that had been a part of the Vale project (Heady and Bartolome 1977).

Management variables recorded were season of use, stocking rate, distance from water (as a proxy for grazing intensity), number of years since most recent seeding and number of years since most recent fire. To determine distance from water we used a combination of field collected records and measurements made from digital BLM records. For each site we also used PRISM (PRISM Climate Group 2014) to estimate precipitation from September in the year the sites were seeded through August of the following year.

4.3.5 Statistics

Step-wise multiple linear regression (JMP® VERSION 10.0.2) was used to select models correlating density of functional groups and species diversity and richness with explanatory variables. Two sets of models were created. The first set of models were developed using all of the sites for which seeding year was available (91 sites) without consideration for grazing. In these models, density of functional groups and species diversity and richness were potentially correlated with seeding age (number of years from recorded seeding date to sampling), time since fire (number of years from recorded time since fire to sampling), precipitation (precipitation from September of the year seeded through August of the subsequent year measured in mm) and their interactions: seeding age x precipitation; seeding age x years since fire; and precipitation x years since fire. The second set of models were developed using the 49 sites that were a) spring-grazed (March 15-May 15; 29 sites) or b) spring-summer-grazed (March 15-August 15; 20 sites). For these models the potential explanatory variables were season (spring = 1 or spring-summer = 0), stocking rate (AUMs·ha^{-1}), distance from water (number of meters from nearest livestock available water) and the interactions: season x stocking rate; season x distance to water; and stocking rate x distance to water. There were, unfortunately, not enough replicates available to evaluate any other seasons of use. Stocking rate was AUMs·ha^{-1} averaged from 2001-2011 including rest years. An average, including rest years, was used in an attempt to capture the long-term grazing pressure on pastures. An initial investigation excluding rest years was not as well correlated with functional groups.

Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrasses (LNPG), annual grasses, perennial forbs, annual forbs, shrubs, Wyoming big sagebrush, Shannon-Weiner diversity (H’) and species richness were used as response variables to perform step-wise multiple linear regression model selection. The explanatory variables were added and deleted in stepwise fashion using p-values to select a parsimonious model that explained the most variation in the response variables resulting in the highest adjusted R^2 value. Factors that did not contribute significantly ($p \leq 0.05$) were excluded from the final model. Data were square root transformed prior to model selection when necessary to better meet linear regression data distribution assumptions.

To determine whether functional group abundance differed between grazed and ungrazed sites, ungrazed sites (n = 6) were blocked with grazed sites (n = 6) that had similar location, soil and time since crested wheatgrass seeding. The same functional and species groups used in model selection were compared between grazed and ungrazed sites using Wilcoxon comparisons (JMP® VERSION 10.0.2).

Functional group and species abundance were compared for the four pre-seeding disturbance methods used on the sites. Because of different sample sizes for the groups, Kruskal-Wallis rank sums was used for comparisons. When there was a difference between groups, Wilcoxon comparisons were used to determine which groups differed (JMP® VERSION 10.0.2).

4.4 RESULTS

4.4.1 Correlations with age of seeding, time since fire and seeding-year precipitation

Shrub foliar cover and density were negatively correlated with seeding year precipitation and were positively correlated with seeding age, time since fire and the interaction between seeding age and time since fire (adj. R^2 = 0.28, 0.28, respectively, $p < 0.001$; Table 4.1 & 4.2). Wyoming big sagebrush foliar cover was negatively correlated with precipitation in the year after seeding and the interaction between precipitation and fire and was positively correlated with seeding age, time since fire and the interaction between seeding age and time since fire (adj. R^2 = 0.34, $p < 0.001$; Table 4.1). Wyoming big sagebrush density was positively correlated with time since fire and was negatively correlated with precipitation in the year after seeding and the interaction between precipitation and time since fire (adj. $R^2 = 0.34$, $p < 0.001$; Table 4.2). Perennial forb cover was weakly correlated with time since fire (adj. $R^2 = 0.11$, $p < 0.001$; Table 4.1).

Age of seeding, time since fire, and precipitation at the time of seeding were not correlated with Shannon-Weiner diversity, species richness, or with basal cover or density of Sandberg bluegrass, large native perennial bunchgrasses, crested wheatgrass, annual grasses, perennial forb density, and annual forbs (adj. $R^2 < 0.10$; $p \geq 0.05$).

4.4.2 Grazing intensity on spring and spring-summer grazed sites

Stocking rate on spring grazed sites averaged 0.020 $\pm$ 0.0019 (mean $\pm$ S.E.) while stocking rate on spring-summer grazed sites averaged 0.042 $\pm$ 0.0042 (mean $\pm$ S.E.). Distance to water on spring grazed sites ranged from 120 to 2900 meters with an average distance of 814 $\pm$ 128 m. Distance to water on spring-summer grazed sites ranged from 330 – 3700 meters with an average distance of 1175 $\pm$ 261 m.

Sandberg bluegrass basal cover and density were negatively correlated with higher stocking rate and with spring only grazing and were positively correlated with longer distance from water and the interaction between stocking rate and distance to water (adj. $R^2 = 0.30$ & 0.27, $p = 0.003$, 0.007, respectively; Table 4.3, 4.4). Increased stocking rates in the spring only grazing plots were negatively associated with large native perennial bunchgrass basal cover and density (adj. $R^2 = 0.37$, 0.37, respectively, $p < 0.0001$; Table 4.3, 4.4).

Crested wheatgrass basal cover was positively correlated with higher stocking rate in spring only grazing sites and the interaction; and was negatively correlated with increasing distance from water, and the interaction between season of use and distance from water (adj. $R^2 = 0.26$, $p < 0.003$; Table 4.3). Crested wheatgrass density was positively correlated with the increasing stocking rate, increasing distance to water and the interaction between stocking rate and distance to water (adj. $R^2 = 0.21$, $p = 0.004$; Table 4.4).

Measured livestock grazing management factors were weakly correlated with exotic annual grass and perennial forb basal cover and density and annual forb density (adj $R^2 > 0.10 < 0.20$; $p < 0.05$; Tables 4.3 & 4.4) and were not correlated with annual forb cover (adj $R^2 < 0.10$; $p > 0.05$).

Total shrub foliar cover was negatively correlated with higher stocking rate, greater distance to water and the interaction between the stocking rate and distance to water (adj. $R^2 = 0.22$; $P = 0.003$; Table 4.3). Higher stocking rates on spring-only grazing sites were negatively correlated with Wyoming big sagebrush foliar cover was with (adj. $R^2 = 0.24$, $p < 0.001$; Table 4.3). Total shrub density and Wyoming big sagebrush density were not weakly correlated with the measured livestock grazing management factors (adj $R^2 < 0.18$, 0.19, respectively; $p < 0.01$; Table 4.4).

4.4.3 Pre-seeding site disturbance

Pre-seeding disturbance affected Sandberg bluegrass density (Figure 4.1; $p < 0.001$, $X^2 = 28.9$). Sandberg bluegrass density was greater on sites that were scarified or herbicide treated than on sites that were burned or plowed ($p < 0.001$) but did not differ between scarified and herbicide treated sites. Sandberg bluegrass basal cover was affected by pre-seeding treatment (Figure 4.2; $X^2 = 26.43$; $p < 0.001$). Sandberg bluegrass basal cover was higher on scarified and herbicide treated sites than on plowed or burned sites ($p \leq 0.001$).

Large native perennial bunchgrass, crested wheatgrass and exotic annual grass density did not differ significantly between pre-seeding treatments ($X^2 = 5.62, 2.68, 1.93$, respectively; $p > 0.05$). Large native perennial bunchgrass, crested wheatgrass and exotic annual grass basal cover did not differ significantly between pre-seeding treatments ($X^2 = 4.42, 5.67, 2.37$, respectively; $p > 0.05$).

Perennial forb density was higher on sites that were scarified or herbicide treated than on sites that were burned prior to seeding (Figure 4.1; $X^2 = 10.90$; $p \leq 0.01$). Other treatments were not significantly different ($p > 0.05$). Perennial forb basal cover did not differ significantly between preseeding treatments (Figure 4.2; $X^2 = 2.49$; $p > 0.05$). Annual forb density and basal cover were higher on plowed and herbicide treated sites than on burned sites (Figure 4.1 & 4.2; $X^2 = 10.90, 8.47$; $p < 0.05$). Other treatments were not significantly different ($p > 0.05$).

Shrub density was higher in scarified and burned treatment sites than on herbicide treated sites (Figure 4.1; $X^2 = 8.21$; $p < 0.05$). Shrub foliar cover was higher on burned sites than on herbicide treated sites ($X^2 = 7.83$; $p < 0.05$). On sites where Wyoming big sagebrush was present, scarified sites had higher Wyoming big sagebrush density than burned or herbicide treated sites (Figure 4.1; $X^2 = 11.3$ $p \leq 0.01$). Density of Wyoming big sagebrush on plowed sites was not statistically different from any of the other treatments. On sites where Wyoming big sagebrush was present, its foliar cover did not differ between treatments (X^2 = 11.29; p > 0.05). Rabbitbrush (*Chrysothamnus viscidiflorus (Hook.) Nutt.*, *Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird*) density and foliar cover were higher on burned sites than on scarified, herbicide treated or plowed sites (Figure 4.1 & 4.2; X^2 = 14.46, 17.74, respectively; p $\leq$ 0.03).Total species diversity and richness did not differ between pre-seeding treatments (X^2 = 6.63; p > 0.05).

4.4.4 Grazed vs ungrazed:

Density of Sandberg bluegrass was 6-times higher (X^2 = 6.89, p = 0.01), large native perennial grasses were 25-times higher (X^2 = 6.39, p = 0.01), perennial forbs were 22-times higher (X^2 = 4.67, p = 0.03), shrubs were 16-times higher (X^2 = 5.31, p = 0.02) and Wyoming big sagebrush was 16-times higher (X^2 = 5.64, p = 0.02) on sites that were grazed than on sites that were not grazed (Figure 4.3). Crested wheatgrass, annual grass and annual forb density did not differ between grazed and ungrazed sites (X^2 = 0.33, 0.41, 0.49, respectively p > 0.10).

Basal cover of Sandberg bluegrass was 4-times higher and large native perennial bunchgrasses were 32-times higher on grazed sites than on ungrazed sites (X^2 = 5.04, p = 0.02; X^2 = 6.37, p = 0.01, respectively; Figure 4.4). Basal cover of crested wheatgrass was higher on ungrazed sites than on grazed sites (X^2 = 5.59, p = 0.02; Figure 4.4). Basal cover of perennial forbs, annual grasses, and annual forbs did not differ between grazed and ungrazed locations (X^2 = 3.47, 0.10, 0.41, respectively; $p > 0.05$). Foliar cover of shrubs was 19-times higher (X^2 = 5.64, p = 0.02) and Wyoming big sagebrush was 14-times higher (X^2 = 5.04, p = 0.02) on grazed than ungrazed sites (Figure 4.4).

4.5 DISSCUSION

Initial conditions and subsequent management of crested wheatgrass seedings can have a major impact on vegetation dynamics. Seeding history, precipitation in the year following seeding and livestock management on crested wheatgrass seedings were important predictors of native vegetation cover and abundance. Precipitation in the year following seeding and disturbance/treatment prior to seeding appear to affect plant community composition in crested wheatgrass stands for decades. Grazed, compared to ungrazed crested wheatgrass stands, appeared to have higher native vegetation and decreased crested wheatgrass monoculture characteristics.

In general, Wyoming big sagebrush cover and density were negatively associated with precipitation in the year following crested wheatgrass seeding. This may be a long-term result of higher initial crested wheatgrass seedling success and lower sagebrush recovery in seeding years with higher than average precipitation (Johnson and Payne 1968; Shown et al. 1969). Mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* (Rydb.) Beetle) recovery depends on how well seedlings establish in the first 2–3 years following fire and although initial germination is largely unrelated to precipitation, subsequent establishment may be higher with higher precipitation (Ziegenhagen and Miller 2009). In crested wheatgrass seedings, higher precipitation in the year following the seeding favors increased crested wheatgrass establishment, thus increasing competition experienced by sagebrush seedlings (Shown et al. 1969; Gunnell et al. 2010). The ability of sagebrush to germinate following disturbance regardless of precipitation and reduced crested wheatgrass establishment in low precipitation years probably helps explain the relationship between lower precipitation and increased sagebrush.

The positive relationship between Wyoming big sagebrush cover and density and time since fire across all sites was in agreement with our expectations. Similarly, other authors have reported that Wyoming big sagebrush is typically slow to recover after fire (Cluff et al. 1983; Wambolt and Payne 1986; Wambolt et al. 2001; Beck et al. 2009). Thus, the greater the time since last fire, the more sagebrush has recovered. Although crested wheatgrass responds positively to fire (Ralphs and Busby 1979) we did not find any evidence suggesting that time since fire was related to current crested wheatgrass cover or abundance.

The majority of the crested wheatgrass seedings for which we were able to obtain actual use records were grazed in the spring or in the spring and summer. On these sites, crested wheatgrass density was positively associated with higher stocking rates while Sandberg bluegrass, large native perennial bunchgrasses and shrubs were negatively correlated with higher stocking rates. This may indicate that crested wheatgrass is responding favorably and native bunchgrasses and shrubs are responding negatively to higher stocking densities as crested wheatgrass is known to be very tolerant to grazing and can withstand heavy grazing for multiple years (Cook et al. 1958; Hull and Klomp

1966, 1974; Caldwell et al. 1981; Laycock and Conrad 1981). However, it is highly probable that the association between stocking rates and crested wheatgrass is a result of higher forage availability in pastures with more crested wheatgrass resulting in greater livestock stocking rates (Dormaar and Smoliak 1985; Smoliak and Dormaar 1985).

Crested wheatgrass basal cover decreased with increased distance from water while crested wheatgrass density was higher with increased distance from water. Thus, fewer large crested wheatgrass plants were closer to water and more small crested wheatgrass plants were further from water, suggesting that grazing pressure was influencing the structural dynamics of crested wheatgrass. The increased basal cover may be a result of increased tiller density as a result of increased tiller growth following herbivory (Caldwell et al. 1981) since crested wheatgrass responds to defoliation in the late spring with increased tiller replacement (Cook et al. 1958; Olson and Richards 1988). The increased density of crested wheatgrass as distance to water increases may be the result of increased seedling survival as livestock become more dispersed leading to more, smaller plants further from water (Salihi and Norton 1987).

Although total shrub and Wyoming big sagebrush cover was lower on sites with higher stocking rates, total shrub cover was higher on sites that were closer to water where livestock pressure is concentrated. Decreased shrub and Wyoming big sagebrush cover in relation to increased stocking rates, and increased crested wheatgrass supports the theory that higher AUMs are a result of higher crested wheatgrass productivity and subsequent increases in stocking rates. Crested wheatgrass productivity is often reduced as a result of increased sagebrush cover (Hull and Klomp 1974; Rittenhouse and Sneva

1976). Wyoming big sagebrush cover was higher on sites that were grazed in the spring through summer than on sites that were only grazed in the spring. The increased shrub cover with greater livestock pressure (i.e. closer to water) and higher sagebrush cover on spring through summer grazed sites is in agreement with prior studies that found increased sagebrush cover under season-long or summer grazing (Robertson et al. 1970; Angell 1997) with little increase in shrub cover on spring grazed sites (Robertson et al. 1970).

Grazed crested wheatgrass seedings had higher shrub cover and density than ungrazed seedings and less crested wheatgrass basal cover. This is consistent with Marlette and Anderson (1986) who found crested wheatgrass maintained a near monoculture for over 50 years in an ungrazed seeding and speculation by Busso and Richards (1995), that intense grazing can create openings in the plant community that allow niche differentiated species such as Wyoming big sagebrush to establish. Crested wheatgrass can inhibit Wyoming big sagebrush and rabbitbrush establishment and growth (Gunnell et al. 2010) and reducing crested wheatgrass cover and density improved sagebrush seedling establishment and growth (Davies et al. 2013). Once established, shrubs are able to coexist with crested wheatgrass and provide a potential seed source for continued shrub establishment (Frischknecht and Harris 1968; Gunnell et al. 2010).

Cover and density of Sandberg bluegrass and large native perennial bunchgrass were negatively associated with higher stocking rates and were positively associated with spring-through-summer grazing. Large native perennial bunchgrasses are typically negatively impacted by intense grazing early in the spring (Strand et al. 2014). Although

Sandberg bluegrass can be more grazing tolerant than many large native bunchgrass species such as bluebunch wheatgrass (Hyder and Sawyer 1951; Krzic et al. 2000), it did not increase with increased stocking rates in the grazed crested wheatgrass seedings. Increased stocking rates are likely indicative of more successful seedings of crested wheatgrass that inherently have less native vegetation. The results from comparing grazed to ungrazed crested wheatgrass stands further suggests that post-hoc regression of native vegetation with stocking rates may not adequately portray the effects of grazing in crested wheatgrass stands. Sandberg bluegrass and large native perennial bunchgrass cover and density were higher on grazed sites than ungrazed sites. This suggests, as with shrubs, that grazing may be beneficial to reduce the competitiveness of crested wheatgrass and to create open spaces where other vegetation can establish (Busso and Richards 1995).

It appears that pre-seeding disturbance affected plant community composition for decades after seeding. Shrub density and foliar cover were higher on burned treatment sites than on herbicide treated sites, largely due to high abundance of rabbitbrush. On sites without sagebrush, rabbitbrush was the most abundant shrub species. Rabbitbrush often recovers quickly following fire because it resprouts (Wambolt et al. 2001) and frequent fire is often associated with increased rabbitbrush density (Bunting et al. 1987). Sites that were treated with herbicide had the lowest shrub abundance which is expected because broadleaf herbicides used to control sagebrush often controlled other shrubs including rabbitbrush (Robertson and Cords 1957; Tueller and Evans 1969). Prior research demonstrated conflicting results with regard to treatments that were most likely to reduce shrub cover. Wambolt and Payne (1986) found that spraying was more effective than burning to reduce sagebrush and, in contrast, Cluff et al. (1983) found that burning was the most effective method for removing Wyoming big sagebrush. We did not find any difference in Wyoming big sagebrush cover or density between burned, sprayed or plowed sites. Wyoming big sagebrush density was higher on scarified sites than on burned or sprayed sites suggesting that more plants either survived scarification or recruitment was greater following scarification than burning or herbicide treatment.

Herbaceous groups also varied considerably by pre-seeding disturbance. Sandberg bluegrass density was highest on plowed sites and lowest on burned sites. Although Sandberg bluegrass is resilient to burning and grazing, it may be shaded out by sagebrush (Acker 1992; Howard 1997). Since shrub cover was highest on burned sites, it is possible that shrubs were negatively influencing Sandberg bluegrass. Perennial forb density was also influenced by pre-seeding disturbance; it was higher on sites that were herbicide treated than on sites that were burned prior to seeding. Spraying herbicides to control sagebrush can have a temporary negative impact on forb production though forbs generally recover within a couple years (Mueggler and Blaisdell 1958; Wambolt and Payne 1986). Annual forb density and basal cover were higher on plowed and herbicide treated sites than on burned sites suggesting that pre-seeding burning had had a long-term negative effect on forbs.

Our data was collected across a variety of sites with variable edaphic, topographic and precipitation characteristics. Even with the large variations across sites, there were predictable effects on vegetation dynamics in association with management and precipitation in the year following seeding. These effects are likely to interact with edaphic factors and disturbances (Shown et al. 1969; Heady and Bartolome 1977; Cluff et al. 1983). Unfortunately, sample sizes prevented us from investigating the role of interactions between the different management influences as well as the role of management in association with environmental site characteristics such as soil texture and topography. In chapter 3 we found that environmental site characteristics were fairly well associated with functional group cover and abundance in crested wheatgrass seedings. Initial seeding success may be influenced by pre-seeding treatment, soil texture and seeding year precipitation (Shown et al. 1969; Cluff et al. 1983). Our results suggest that some of these effects may persist for decades and that further investigation of the role of interaction between soil texture and management may be warranted. Our results also suggest that grazing influenced the cover and abundance of native vegetation in crested wheatgrass seedings and that continued research into levels and timing of grazing on the effects of native plant abundance in crested wheatgrass stands is necessary and may prove invaluable in assisting efforts to diversify crested wheatgrass stands.

4.6 FIGURES

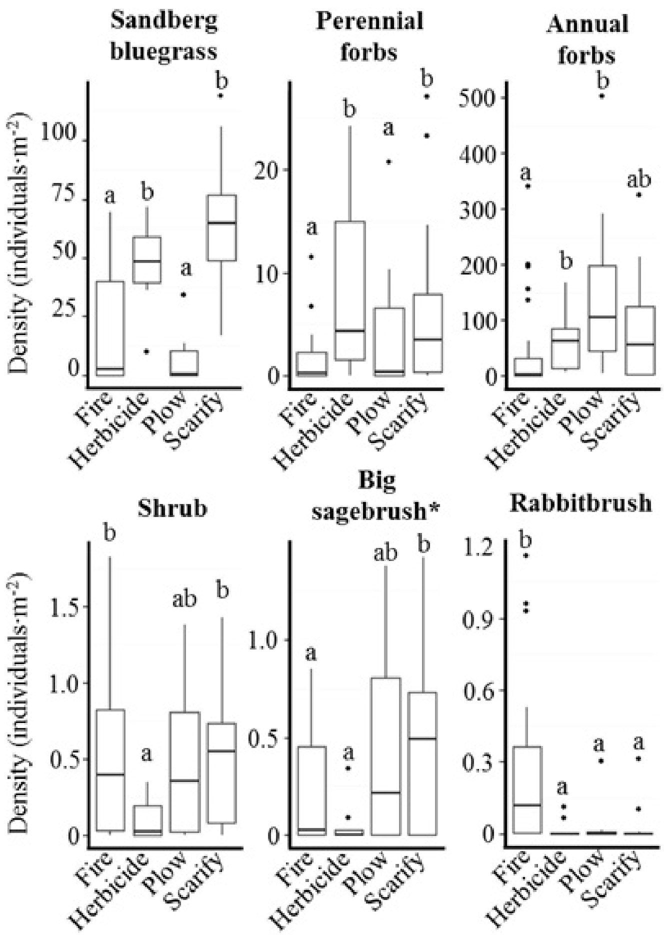

Figure 4.1. Density (individuals·m^{-2}) of Sandberg bluegrass, perennial forbs, annual forbs, shrubs, Wyoming big sagebrush* and rabbitbrush on sites that were burned (n = 31), herbicide treated (n = 9), plowed (n = 8), or scarified (n = 15) prior to seeding crested wheatgrass. *Wyoming big sagebrush was compared on sites only where it was present (n = 24, 5, 6, 10, respectively). Functional groups and species were compared shown are significant at $p < 0.05$ using Kruskal-Wallis rank sum comparisons. Different letters indicate significant differences at $p < 0.05$.

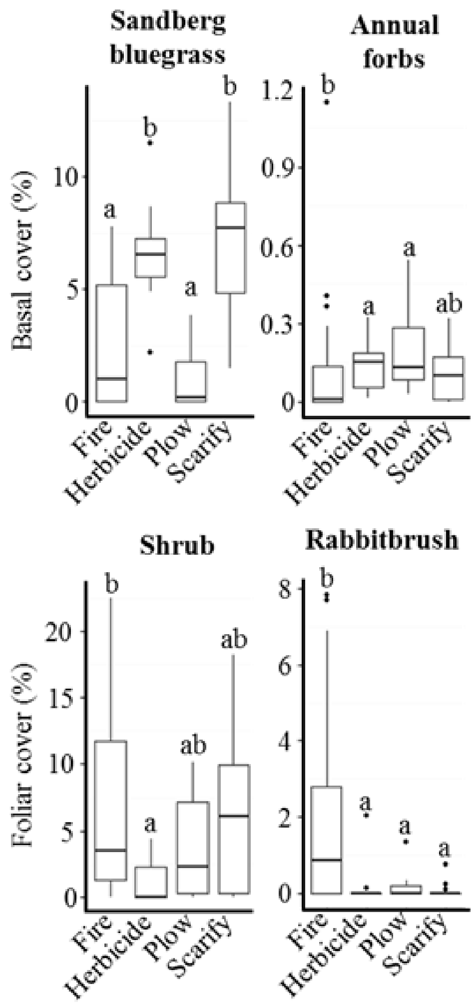

Figure 4.2. Basal cover (%) of Sandberg bluegrass and annual forbs, and foliar cover (%) shrubs and rabbitbrush on sites that were burned (n = 31), herbicide treated (n = 9), plowed (n = 8), or scarified (n = 15) prior to seeding crested wheatgrass. Functional groups and species were compared shown are significant at $p < 0.05$ using Kruskal-Wallis rank sum comparisons. Different letters indicate significant differences at $p < 0.05$.

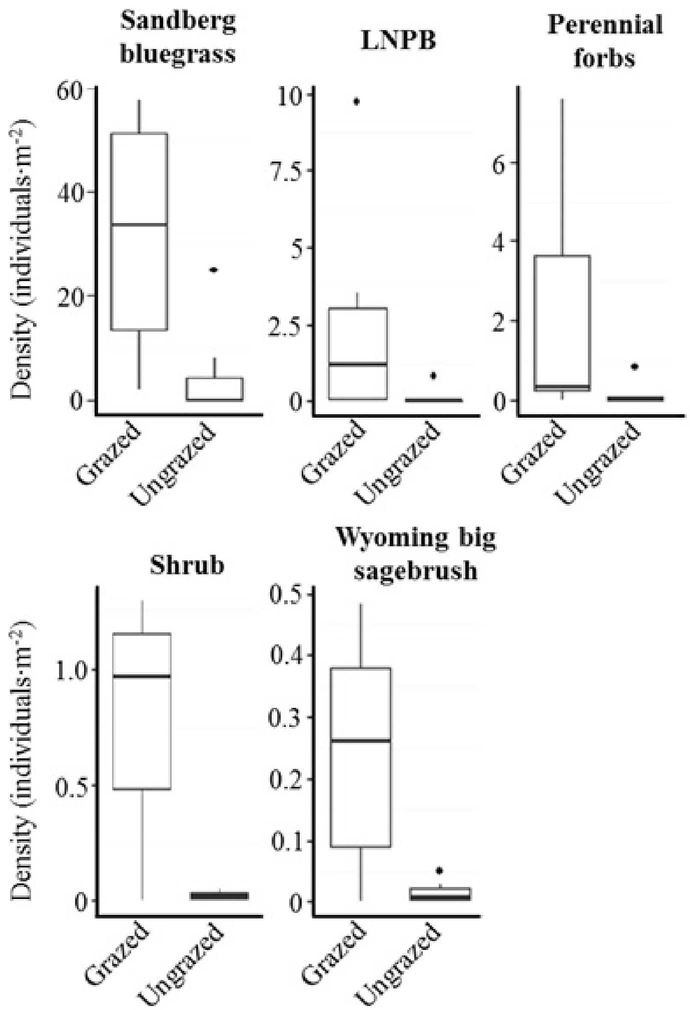

Figure 4.3. Density (individuals·m^{-2}) of Sandberg bluegrass, large native perennial bunchgrasses (LNPB), perennial forbs, shrubs and Wyoming big sagebrush on crested wheatgrass seedings that were grazed (n = 6) or ungrazed (n = 6). Grazed and ungrazed sites had similar soil texture, location, seeding age and time since fire. Shown grazed and ungrazed functional groups and species were compared using Wilcoxon rank sums and were significantly different at $p < 0.05$.

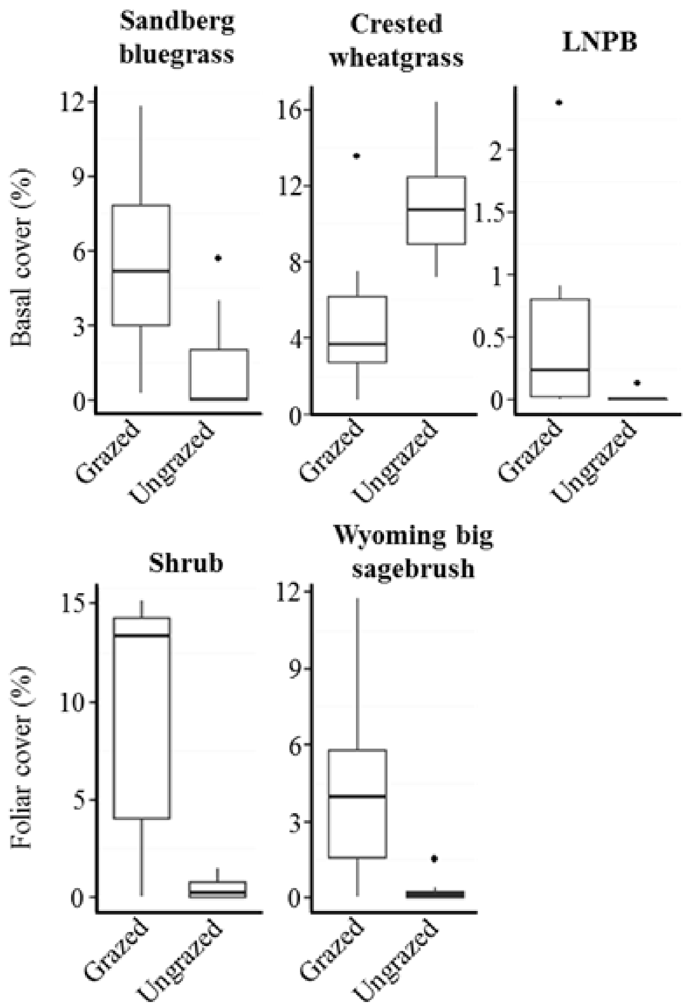

Figure 4.4. Basal cover (%) of Sandberg bluegrass, crested wheatgrass, and large native perennial bunchgrasses (LNPB) and foliar cover (%) of shrubs and Wyoming big sagebrush on crested wheatgrass seedings that were grazed (n = 6) or ungrazed (n = 6). Grazed and ungrazed sites had similar soil texture, location, seeding age and time since fire. Shown grazed and ungrazed functional groups and species were compared using Wilcoxon rank sums and were significantly different at $p < 0.05$.

4.7 TABLES

Table 4.1. Stepwise multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrass (LNPB), annual grass and annual forb basal cover (%) and shrub functional group and Wyoming big sagebrush (ArtrWy) foliar cover (%) with historic site characteristics. Standard errors in parentheses below coefficients. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only regression equations with adj. $R^2 > 0.10$ are shown. Adj. $R^2 > 0.20$ are indicated by bold text.[1]

Functional Group (% Cover)	Adj R^2	Intercept	Age	YFire	PPT	Age* YFire	Age* PPT	YFire* PPT	P-value
Sandberg bluegrass	—	—	—	—	—	—	—	—	—
Crested wheatgrass	—	—	—	—	—	—	—	—	—
Sqrt (LNPB)	—	—	—	—	—	—	—	—	—
Sqrt (Annual grass)	—	—	—	—	—	—	—	—	—
Sqrt (Perennial forb)	0.11	+ 0.071 (0.083)		+ $3.4e^{-3}$ ($9.9e^{-4}$)					< 0.001
Sqrt (Annual forbs)	—	—	—	—	—	—	—	—	—
Sqrt (Shrubs)	**0.28**	+ 3.16 (0.80)	+ $6.4e^{-3}$ (0.013)	+ $7.3e^{-3}$ ($3.7e^{-3}$)	− $8.0e^{-3}$ ($1.9e^{-3}$)	+ $1.1e^{-3}$ ($3.8e^{-4}$)			< 0.001
Sqrt (ArtrWy)	**0.34**	+ 3.16 (0.80)	+ 0.013 (0.012)	+ 0.012 ($3.9e^{-3}$)	− $7.5e^{-3}$ ($1.8e^{-3}$)	+ $8.0e^{-4}$ ($3.6e^{-4}$)		− $1.7e^{-4}$ ($5.1e^{-5}$)	< 0.001

[1]Age = Number of years from the year crested wheatgrass was last seeded to the sampling year;
YFire = Number of years from the last recorded fire following crested wheatgrass seeding to the sampling year. Sites without fire were given a value of 100;
PPT = Total precipitation from September 1 of the year crested wheatgrass was seeded to August 31 of the following year in mm.

Table 4.2. Stepwise multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrass (LNPB), annual grass and annual forb and shrub functional group and Wyoming big sagebrush (ArtrWy) density (plants·m^{-2}) with historic site characteristics. Standard errors in parentheses below coefficients. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only regression equations with adj. $R^2 > 0.10$ are shown. Adj. $R^2 > 0.20$ are indicated by bold text.[1]

Functional Group (plants·m^{-2})	Adj R^2	Intercept	Age	YFire	PPT	Age*YFire	Age*PPT	YFire*PPT	P-value
Sandberg bluegrass	0.19	– 4.71 (11.99)	+ 1.21 (0.29)	– 0.18 (0.077)		– 0.025 ($8.3e^{-3}$)			0.001
Crested wheatgrass	–	–	–	–	–	–	–	–	–
Sqrt (LNPB)	–	–	–	–	–	–	–	–	–
Sqrt (Annual grass)	0.13	+ 9.89 (3.91)		– 0.014 (0.02)	– $7.4e^{-3}$ (0.01)			+ $1.1e^{-3}$ ($2.9e^{-4}$)	0.002
Sqrt (Perennial forb)	–	–	–	–	–	–	–	–	–
Sqrt (Annual forbs)	–	–	–	–	–	–	–	–	–
Sqrt (Shrubs)	**0.28**	+ 0.85 (0.23)	+ $2.4e^{-3}$ ($3.8e^{-3}$)	+ $2.5e^{-3}$ ($1.1e^{-3}$)	– $2.2e^{-3}$ ($5.4e^{-4}$)	+ $2.6e^{-4}$ ($1.1e^{-4}$)			< 0.001
Sqrt (ArtrWy)	**0.34**	+ 0.63 (0.18)		+ $3.3e^{-3}$ ($9.8e^{-4}$)	– $2.0e^{-3}$ ($4.8e^{-4}$)			– $3.6e^{-5}$ ($1.4e^{-5}$)	< 0.001

[1]Age = Number of years from the year crested wheatgrass was last seeded to the sampling year;
YFire = Number of years from the last recorded fire following crested wheatgrass seeding to the sampling year. Sites without fire were given a value of 100;
PPT = Total precipitation from September 1 of the year crested wheatgrass was seeded to August 31 of the following year in mm.[1]

Table 4.3. Stepwise multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrass (LNPB), annual grass and annual forb basal cover (%) and shrub functional group and Wyoming big sagebrush (ArtrWy) foliar cover (%) in spring & spring-summer grazed sites. Standard errors in parentheses below coefficients. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Only regression equations with adj. $R^2 > 0.10$ are shown. Adj. $R^2 > 0.20$ are indicated by bold text.[1]

Functional Group (% Cover)	Adj R^2	Intercept	AUM	H_2O	Season	AUM* H_2O	AUM* Season	H_2O* Season	P-value
Sandberg bluegrass	**0.30**	+ 5.73 (1.38)	– 49.33 (28.10)	+ $6.1e^{-4}$ ($4.3e^{-4}$)	– 2.08 (0.98)	+ 0.094 (0.039)			0.003
Crested wheatgrass	**0.26**	+ 0.38 (1.76)	+ 169.49 (42.01)	– $7.6e^{-4}$ ($3.6e^{-4}$)	+ 2.67 (1.26)		+ 186.92 (76.99)	– $3.8e^{-3}$ ($1.2e^{-3}$)	0.003
Sqrt (LNPB)	**0.37**	+ 0.77 (0.17)	– 20.23 (4.18)		– 0.081 (0.13)		– 28.82 (7.69)		< 0.001
Sqrt (Annual grass)	0.12	+ 0.10 (0.10)		+ $1.1e^{-4}$ (6.4^{-5})	+ 0.21 (0.10)			+ $2.9e^{-4}$ ($1.1e^{-4}$)	0.03
Sqrt (Perennial forb)	0.19	+ 0.96 (0.17)	– 12.76 (3.55)		– 0.34 (0.12)				0.003
Sqrt (Annual forbs)	–	–	–	–	–	–	–	–	–
Sqrt (Shrubs)	**0.22**	+ 3.38 (038)	– 37.76 (10.58)	– $1.1e^{-4}$ ($1.9e^{-4}$)		– 0.045 (0.018)			0.003
Sqrt (ArtrWy)	**0.24**	+ 3.38 (0.59)	– 60.47 (14.63)		– 0.69 (0.45)		– 69.11 (26.91)		< 0.001

[1]AUM: Average AUMs·ha^{-1} from 2001 – 2011 including rest years;
H_2O: Meters from nearest livestock available water;
Season: 0 = Spring-summer (March 15 – September 15) grazing; 1 = Spring (March 15 – May 15) grazing

Table 4.4. Stepwise multiple linear regression models for Sandberg bluegrass, crested wheatgrass, large native perennial bunchgrass (LNPB), annual grass, annual forb, shrub functional group and Wyoming big sagebrush (ArtrWy) density (plants·m^{-2}) in spring & spring-summer grazed sites. Variables were square root (Sqrt) transformed when necessary to meet model assumptions. Standard errors in parentheses below coefficients. Only regression equations with adj. $R^2 > 0.10$ are shown. Adj. $R^2 > 0.20$ are indicated by bold text.[1]

Functional Group (plants·m^{-2})	Adj R^2	Intercept	AUM	H_2O	Season	AUM*H_2O	AUM*Season	H_2O*Season	P-value
Sandberg bluegrass	**0.27**	+ 48.05 (11.25)	− 449.61 (228.71)	+ $4.1e^{-3}$ ($3.5e^{-3}$)	− 17.63 (7.95)	+ 0.66 (0.32)			0.007
Crested wheatgrass	**0.21**	+ 4.22 (1.25)	+ 110.13 (35.09)	+ $4.2e^{-4}$ ($6.4e^{-4}$)					0.004
Sqrt (LNPB)	**0.37**	+ 1.63 (0.31)	− 38.98 (7.53)		− 0.32 (0.23)		− 46.74 (13.84)		0.001
Sqrt (Annual grass)	0.19	+ 1.21 (1.60)		+ $2.4e^{-3}$ (9.8^{-4})	+ 2.93 (1.60)			$6.0e^{-3}$ ($1.8e^{-3}$)	0.005
LN (Perennial forb)	0.15	+ 2.43 (0.70)	− 38.34 (14.81)		− 1.66 (0.54)				0.009
Sqrt (Annual forbs)	0.11	+ 8.88 (1.18)			− 3.96 (1.53)				0.01
Sqrt (Shrubs)	0.19	+ 1.20 (0.19)	− 12.45 (3.71)	− $4.2e^{-5}$ $6.4e^{-5}$)				+ $2.2e^{-4}$ ($1.2e^{-4}$)	0.01
Sqrt (ArtrWy)	0.18	+ 0.95 (0.17)	− 14.89 (4.08)		− 0.25 (0.13)		− 12.79 (7.50)		0.008

[1] AUM: Average AUMs·ha^{-1} from 2001 – 2011 including rest years;
H_2O: Meters from nearest livestock available water;
Season: 0 = Spring-summer (March 15 – September 15) grazing; 1 = Spring (March 15 – May 15) grazing

5 General Conclusions

Native vegetation presence is highly variable within crested wheatgrass seedings. Near-monocultures of crested wheatgrass existed but some stands had relatively abundant native vegetation, especially shrubs. We found that big sagebrush was the most common native shrub species in stands of crested wheatgrass, a result supported by others (Hull and Klomp 1966; Marlette and Anderson 1986; Krzic et al. 2000). It is important to identify factors associated with increased Wyoming big sagebrush in crested wheatgrass seedings since it is a foundation species (Prevey et al. 2010) that is critical to the presence and diversity of sagebrush obligate wildlife species (Knick et al. 2003). We found that Wyoming big sagebrush occurred on 63% of the sampled sites and made up 72% of overall shrub cover. A variety of site factors helped explain the variability in Wyoming big sagebrush; it was positively associated with silty soils, time since fire, and decreased precipitation in the year following crested wheatgrass seeding.

Native vegetation is more likely to coexist with crested wheatgrass on finer-textured soils. Native bunchgrasses have higher abundances on silty-textured soils. However, even on a silt loam soil where native bunchgrasses and crested wheatgrass were simultaneously established at evenly-dispersed, low densities, we saw a 10-fold increase in crested wheatgrass density and a decrease in half of the native bunchgrass species. Although 10% of our sampled sites had a higher density of native perennial bunchgrasses than crested wheatgrass, we found, overall, few large native perennial bunchgrasses in most stands of crested wheatgrass. Native perennial bunchgrasses do not generally increase on sites when seeded or planted in conjunction with non-native perennial grass species such as crested wheatgrass (Knutson et al. 2014; Nafus et al. 2015) and are frequently outcompeted by crested wheatgrass (Bakker and Wilson 2001). Native perennial bunchgrasses can be difficult to establish in crested wheatgrass dominated plant communities, even with management to reduce crested wheatgrass (Hulet et al. 2010; Fansler and Mangold 2011). Overall we found a limited abundance of native perennial bunchgrasses in crested wheatgrass seedings and a failure of native perennial bunchgrasses to increase even when successfully established at low densities alongside crested wheatgrass. This raises the question of how effective simultaneous seedings of crested wheatgrass and native bunchgrasses might be if the management objective is for native vegetation to establish and increase.

Grazing management affected the interactions of crested wheatgrass and native vegetation functional groups in several possible ways. Moderate grazing of crested wheatgrass seedings was associated with increased cover and density of native vegetation functional groups relative to ungrazed seedings. However, we also found negative associations between native vegetation cover and density and higher stocking rates. We postulate that stocking rates were not able to accurately reflect grazing pressure on native vegetation. The positive relationship between higher AUMs and increased crested wheatgrass cover and density and decreased native vegetation cover and density is most likely a product of increased stocking rates on sites with greater crested wheatgrass productivity and lower shrub cover.

The results suggest that without active management, crested wheatgrass stands are likely to have low diversity of native vegetation. It may be possible to develop grazing strategies to diversify crested wheatgrass stands and some sites appear more likely to respond positively to treatments than other sites. Although our results indicate that grazing management can be used to diversify stands of crested wheatgrass, further research is required to identify the best management strategies.

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