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Clarifying Potential Successional Trajectories in Sagebrush Communities Historically Seeded with Crested Wheatgrass

Kevin L. Gunnell¹, Justin R. Williams², and Thomas A. Monaco²

ABSTRACT

Crested wheatgrass (Agropyron cristatum [L.] Gaertn.) has been historically seeded on thousands of ha of Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis) communities. Initially used to improve degraded rangeland, its use has become controversial in the current management setting where emphasis has shifted from increased forage production to increased community diversification. Naturalized crested wheatgrass communities are an attractive setting for this goal of diversification, but little is understood about how succession proceeds in the absence of management techniques that perpetuate the dominance of crested wheatgrass, in other words, fire, chemical, and mechanical treatments. Further research in communities that have not experienced these treatments may help define interacting factors, determine successional trajectories, and provide insights into management options to satisfy contemporary and future rangeland management activities within seeded Wyoming big sagebrush communities.

INTRODUCTION

Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is an exotic perennial bunchgrass that has been seeded on thousands of ha in the Great Basin. These seeded communities represent one of the largest-scale land management manipulations within sagebrush-steppe ecosystems. Pervasive overgrazing across this ecosystem diminished native herbaceous plant cover and promoted dense stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) and the opportunity for weed invasion (Young and others 1999). In the early 1950s, large-scale preventative measures were taken to control the spread of the poisonous weed halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.) (Mathews 1986). Federal appropriations were granted to government agencies to prevent further expansion of halogeton and other weeds, improve forage potential, reduce fire frequency, and stabilize soil resources of these degraded landscapes (Blaisdell and others 1982; Mathews 1986). Crested wheatgrass was a primary tool used to accomplish this goal (Young and Evans 1986). Since the 1970s, crested wheatgrass has been planted on private and public lands in the Great Basin primarily following wildfires to maintain rangeland productivity, and reduce the spread of invasive

annual species including downy brome (*Bromus tectorum* L.), Russian thistle (*Salsola kali* L.), tumble mustard (*Sisymbrium altissimum* L.) and medusahead rye (*Taeniatherum caput-medusae* [L.] Nevski). Hundreds of articles were published in scientific journals between 1950 and 1980 on management implications of crested wheatgrass communities. The majority of these articles focused on methodologies to properly manage these communities for forage production while preventing sagebrush from reinvading. In our contemporary era of rangeland management, emphasis has shifted to include stabilization and restoration of shrub-steppe communities. Current rangeland rehabilitation emphases include reducing wildfire frequency, improving species diversity, improving critical winter habitat for big game species, and protecting habitat for threatened and endangered wildlife species (Pellant and Lysne 2005).

Wyoming big sagebrush communities seeded with crested wheatgrass are a particularly attractive setting to improve Great Basin plant communities because they are characteristically more stable and less fire-prone than downy brome-dominated communities. While some studies have evaluated reseeding native species into crested wheatgrass-dominated communities (Bakker and others 1997; Bakker and Wilson 2001; Fansler 2007), studies on the ability of native species to naturally re-establish are lacking. Today, vast landscapes within the Great Basin contain or are dominated by crested wheatgrass. The continued use of crested wheatgrass is controversial because the long-term ecological consequences of its use within this ecosystem are unknown. In addition, while landscapes were stabilized and forage potential was improved by crested wheatgrass, these historic seedings have not been comprehensively characterized to determine their vegetative and seed bank composition, structure, or functional attributes. Specifically, this extensive land-management treatment has not been adequately assessed in terms of the multiple interacting factors that determine vegetation and seed bank attributes and successional trajectories. Filling these gaps in knowledge may provide a mechanistic understanding of the factors limiting natural reinvasion by native species and help overcome the challenges associated with diversifying crested wheatgrass communities. We provide this literature review to address these issues and discuss what is known and directions that further research might take.

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Brief History of Great Basin Vegetation

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

Pre-settlement composition of vegetation is difficult to predict for many reasons. The first explorers in the Great Basin emphasized the dominance of sagebrush. Historical ecology also confirms sagebrush dominance (Rogers 1982; Vale 1975); however, some locations may have been grass-dominated (Hull and Hull 1974). Variability in vegetation dominance in Great Basin sagebrush communities has been attributed to dynamic variation in fire frequency, climate, and herbivory (Egan and Howell 2001; Knight 1994; Mack and Thompson 1982; Swetnam and others 1999; West and Yorks 2006; Wright 1985).

Considerable evidence exists indicating that regardless of sagebrush dominance, native grass and forb abundance has drastically declined (Johnson 1989; West 1988). Since large herbivores were not present in numbers to adversely impact herbaceous species, the decline in abundance has been attributed to poor grazing tolerance and the absence of intensive ungulate herbivory prior to European settlement (Mack and Thompson 1982). Wildfires did occur, and because herbaceous species have the potential to readily regrow while sagebrush does not (Wright 1985), wildfire functioned as an ecosystem driver to determine relative abundances of sagebrush and herbaceous cover (Bork and others 1998; Harniss and Murray 1973; Kay 1960; Monsen 1994; Wright 1985).

Fire frequency within sagebrush-steppe ecosystems has also changed considerably since European settlement. Changes in fire frequency were initiated as a consequence of invasive annual grasses replacing native herbaceous species (Monsen 1994; Young and Evans 1973). Foremost among these annual grasses are downy brome and medusahead (*Taeniatherum caput-medusae* (L.) Nevski), which produce high amounts of fine-fuels that carry fire more readily than native species (Whisenant 1990; Young and Evans 1973). The spread and dominance of annual weeds produced larger wildfires and perpetuated further expansion of annual weed infestations. Introduction of livestock grazing and annual weed-mediated changes in wildfire frequency greatly reduced the forage potential of sagebrush-steppe ecosystems (Griffiths 1903; Pickford 1932; Tournay 1894).

Consequently, land management efforts attempted to end the misuse of sagebrush-steppe rangelands in the early 1900s (Stoddart and Smith 1955); however, overgrazing and wildfire continued to alter this ecosystem well into the twentieth century because of the demand for livestock production (Chatterton and Young 2002; Young 1994). In this era, improving the forage potential of these lands was the primary goal of resource managers (Young and Evans 1986).

Introduction of Crested Wheatgrass Into The Great Basin

Identifying forage grasses to improve rangeland productivity was the research emphasis of early American range researchers such as P.B. Kennedy and A.W. Sampson at the turn of the 20th century (Chatterton and Young 2002). Many exotic grasses, including crested wheatgrass performed better than the available native species, and became the “gold standard” to use on former shrub-steppe and sagebrush rangelands (Young and McKenzie 1982). Crested wheatgrass was first introduced into the Northern Great Plains from Russia in 1898 and was later promoted as a successful revegetation species suitable for the needs of land managers (Dillman 1946; Rogler and Lorenz 1983; Young and Evans 1986). The first seeding evaluations in the northern Great Basin and Snake River Plain were made in the early 1930s (Hull and Klomp 1966). Reclamation of abandoned dry-land farms and unproductive sagebrush pastures on private and public land prompted government researchers to publish bulletins on how to reseed these rangelands in Nevada, Idaho, and Utah in the early 1940s (Pellant and Lysne 2005; Young and Evans 1986). Less productive sagebrush-steppe grazing areas were plowed and seeded with crested wheatgrass to increase forage production, promote the rehabilitation of degraded rangelands, and increase meat production to support the World War II effort (Young and Evans 1986). Eventually, the use of crested wheatgrass greatly expanded in 1952 with the Halogeton Control Act, a program designed to stop the spread of the poisonous, annual weed halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.) by seeding crested wheatgrass throughout the Great Basin and beyond (Young and Evans 1986).

Establishing crested wheatgrass required modifying traditional agricultural techniques to fit a new set of obstacles associated with seedings on rough rangelands. Developing the rangeland drill and brushland plow effectively allowed sagebrush removal and large seedings over rough terrain (Young and McKenzie 1982). Large-scale seedings continued until the 1970s, when crested wheatgrass became the focus of controversy (Chatterton and Young 2002; Pellant and Lysne 2005). This controversy stemmed from the perception that crested wheatgrass may be responsible for low quality wildlife habitat and diminished native plant diversity (Dobkin and

Sauder 2004; Wilson 1989). Thus, federal agencies were encouraged to use native species in new seeding projects when feasible depending on availability, cost, and potential success for establishment (Pellant and others 2004; Pellant and Lysne 2005). Crested wheatgrass is still used in large-scale seedings on public land, but is now a component of a more diverse seed mix that includes native species (Pellant and Lysne 2005). The underlying issue today is that crested wheatgrass exists on millions of has of public and private rangelands and is a persistent, naturalized component of plant communities where it was established in the past.

As the need to reclaim degraded rangelands increased, the production of crested wheatgrass seed also increased (Sharp 1986). Thus, in addition to being easier to establish than native grasses, plentiful seed availability also led to its preference for rangeland seedings. Good seedling vigor makes crested wheatgrass ideal for reclamation because it is very competitive with slower growing species, is drought tolerant, and has an efficient nutrient acquiring root system (Bakker and Wilson 2001; Caldwell and others 1991; Eissenstat and Caldwell 1988). In addition, crested wheatgrass is competitive with weedy species and reduces downy brome dominance better than native species because it germinates earlier and grows more rapidly at colder temperatures (Chatterton and Harrison 2003). Crested wheatgrass is long-lived and perpetuates stable populations primarily by good seed production (Marlette and Anderson 1986). Forage production is two-fold greater than native range in shrub-steppe ecosystems with limited precipitation (Angell and others 1990; Gade and Provenza 1986; Ganskopp and others 1997; Laycock and Conrad 1981; Springfield and others 1967). Crested wheatgrass is also known to have superior drought tolerance (Caldwell and Richards 1986; Sharp and others 1992) and can persist under drought conditions in semi-arid environments (Busso and others 1990; Currie and Peterson 1966). In general, crested wheatgrass can withstand heavy grazing (Angell 1997; Caldwell and others 1991; Cook and others 1958; Laycock and Conrad 1981; Sharp 1986) with some limitations (Sharp 1970). Because crested wheatgrass evolved with ungulate grazing pressure, it is well adapted to higher utilization levels than native Great Basin grasses (Sharp 1986). Crested wheatgrass can withstand intense biomass removal because of its ability to re-establish pre-defoliation leaf area and high compensatory photosynthesis (Frischknecht and Harris 1968; Olsen and Richards 1988).

Succession in Sagebrush Communities Seeded With Crested Wheatgrass

Early research on crested wheatgrass management focused on grazing and fire as well as other mechanical and chemical treatments to maintain crested wheatgrass productivity and dominance (Evans and Young 1978; Hull 1974; Klomp and Hull 1972; McLean and van Ryswyk 1973; Mueggler and Blaisdell 1958). Although crested

wheatgrass reduces shrub seedling invasion more than native grasses (Blaisdell 1949; Frischnecht and Bleak 1957; Schuman and others 1982), without fire and subsequent management treatments, sagebrush reinvades over time (Frischknecht and Bleak 1957; Hull and Klomp 1966). A review of these management activities is a necessary and preliminary step to determine the potential of seedings to establish as stable crested wheatgrass stands or be reinvaded by native sagebrush-steppe species from adjacent plant communities (Johnson and Payne 1968).

Livestock grazing practices, including intensity, duration, season, and animal type impact plant succession in sagebrush communities seeded with crested wheatgrass (Holechek and others 1995; Pieper 1994). Crested wheatgrass dominance is maintained, and sagebrush encroachment is reduced, by heavy autumn grazing more so than spring grazing (Frischknecht and Harris 1968; Hull and Klomp 1974; Laycock and Conrad 1981; Robertson and others 1970). In addition, sheep versus cattle grazing of crested wheatgrass reduces shrub encroachment (Blaisdell and others 1982; Bleak and Plummer 1954; Laycock and Conrad 1981). Livestock grazing can also directly reduce shrub invasion by trampling seedlings (Owens and Norton 1992). Conversely, livestock grazing practices can also promote sagebrush reinvasion, particularly prolonged spring grazing during drought (Busso and Richards 1995). Over-utilization of crested wheatgrass through high intensity, long-duration grazing reduces grass productivity and enhances seedling survival of other species including sagebrush (Angell 1997; Salihi and Norton 1987). Grazing crested wheatgrass in the spring reduces its dominance and may allow invasion of shrub species (Laycock and Conrad 1981; Olsen and Richards 1988; Robertson and others 1970). However, regardless of grazing, and without periodic treatments to reduce sagebrush, it is capable of reinvading crested wheatgrass seedings (Astroth and Frischknecht 1984; Torell 1986).

Management activities that directly kill shrub and herbaceous dicotyledonous species have obvious impacts on maintaining crested wheatgrass dominance. The absence of fire and brush removal treatments (chemical and mechanical) allows crested wheatgrass seedings to be reinvaded by native sagebrush-steppe species from adjacent plant communities. Prescribed fire perpetuates crested wheatgrass dominance because it has a high post-burn recovery and productivity, whereas sagebrush is killed (Harniss and Murray 1973; Kay 1960; Lodge 1960; Wright 1985). Mechanical treatments, including plowing, disking, chaining, mowing, and the use of pipe harrows, rails, and cables effectively reduce shrub abundance and density, and facilitate herbaceous dominance (Blaisdell and others 1982; Lodge 1960; Mueggler and Blaisdell 1958; Parker 1979; Pechanec and others 1965; Vallentine 1989; Wambolt and Payne 1986; Young and McKenzie 1982). Finally, chemical

control with 2, 4-D and tebuthiuron successfully reduces shrub density and increases crested wheatgrass dominance (Astroth and Frischknecht 1984; Cox and Anderson 2004; Eckert and others 1972; Evans and others 1979; Holechek and others 1995; Johnson and Payne 1968; Pellant and Lysne 2005). The effectiveness of these treatments to maintain crested wheatgrass dominance is also determined by their season of application (Blaisdell and others 1982; Evans and Young 1978).

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

Seed Bank Dynamics of Sagebrush Communities Seeded With Crested Wheatgrass

Seed banks provide important insights into plant community dynamics including colonization and succession (Bazzaz 1979), population structure (Wilson 1992), and community structure (Yarranton and Morrison 1974). Seed banks are characterized by their horizontal and vertical distribution within the soil and litter, and temporally according to the timing of seed rain input and seed longevity (Freas and Kemp 1983; Kemp 1989; Reichman 1975; Williams and others 1974; Young and Evans 1975). Transient seed banks are viable for less than 1 year and therefore rely on seed rain input to maintain a presence in the seed bank, while persistent seed banks are viable longer than 1 year and can persist in the seed bank without further seed rain input (Thompson and Grime 1979). In general, seed banks of annual species are more persistent than

perennial species in arid and semiarid ecosystems (Kemp 1989). No studies were found that addressed how the seed banks of sagebrush communities seeded with crested wheatgrass were horizontally or vertically distributed, but the temporal distribution of crested wheatgrass was less variable than the native bluebunch wheatgrass (Pyke 1990). While bluebunch wheatgrass released all of its seed upon maturation, crested wheatgrass retained seed in the inflorescence and released them into the following spring. This helped crested wheatgrass to maintain a viable seed bank throughout the growing season and to protect its seed from predation (Pyke 1990). It was also observed that ungerminated crested wheatgrass seeds stayed viable in the seed bank from the first to second year of the study (Pyke 1990).

There is still little known about seed bank composition and its impact on succession within Wyoming big sagebrush communities seeded with crested wheatgrass over a broad representative area. Composition of seed banks in semi-arid ecosystems seeded with crested wheatgrass generally resembles the current aboveground vegetation (Ambrose and Wilson 2003; Henderson and others 1988; Henderson and Naeth 2005; Marlette and Anderson 1986; Pyke 1990). The high seed productivity of crested wheatgrass (Pyke 1990) and the transient nature of the seed bank of many native species in these communities can create a negative feedback that perpetuates crested dominance in the seed bank. The density of crested wheatgrass seeds in the seed bank of sagebrush communities seeded with crested wheatgrass was typically much higher than for other species. Pyke (1990) observed densities of 1,772 to 1,037 seeds m^{-2} and 26 to 0 seeds m^{-2} for crested wheatgrass and bluebunch wheatgrass, respectively, for two years of the study (1986 to 1987). Marlette and Anderson (1986) showed similar dominance of crested wheatgrass in the seed bank, with 84.67 to 92.28 percent of low diversity stands and 31.91 to 72.79 percent in sagebrush re-invaded communities. Crested wheatgrass may also dominate seed banks of these communities because of the lack of a seed source and the poor dispersal of native species (Marlette and Anderson 1986). Seed bank composition, or more specifically, seed density of species, may exert some control over successional trajectories of plant communities through its effects on interference between emerging seedlings (Francis and Pyke 1996; Sheley and Larson 1994; Velagala and others 1997). When crested wheatgrass dominates seed banks, it may have a disproportionate impact on seedling emergence and establishment of native species because of the well-recognized advantages for seedling performance of crested wheatgrass (Bakker and Wilson 2001; Caldwell and others 1991; Eissenstat and Caldwell 1988; Harris and Wilson 1970).

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

IMPLICATIONS

Crested wheatgrass was initially adopted to restore the productivity of depleted rangelands. However, there are concerns about low diversity and the long-term effects introduced plants have on native landscapes, in particular, wildlife habitat, soil quality, and ability to resist invasive weeds (Dobkin and Sauder 2004; Dormaar and others 1995; Holechek 1981; Wilson 1989). Many of these concerns are based on the lack of research in historic (> 30 year-old) crested wheatgrass seedings. Therefore, addressing important issues involving these seeded communities may help managers make important decisions for future management. Do seeded Wyoming big sagebrush communities remain dominated by crested wheatgrass and resistant to weed invasion? What is the variability in species abundance and diversity in old crested wheatgrass seedings, and are they functionally different than native sagebrush-steppe rangelands managed similarly? Is the perception of low plant diversity in crested wheatgrass seedings an artifact perpetuated by obvious management activities and pre-seeding soil attributes that favor crested wheatgrass dominance? Is resilience of crested wheatgrass caused by seed limitation of native species or competitive exclusion of seeds that arrive? What is the role of grazing on plant species diversity, relative to the factors of soil and climate? These issues can be addressed through the practical approach of evaluating the relationships between multiple interacting factors, in other words, vegetation, grazing history, soil properties, climate, topography, and seed banks on Wyoming big sagebrush communities historically seeded with crested wheatgrass that have not experienced fire or other mechanical and chemical treatments. Further research to address these questions may help define how these multiple interacting factors determine successional trajectories and provide insights into

management options to satisfy contemporary and future rangeland management activities within seeded Wyoming big sagebrush communities.

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