Cheatgrass invasions:
History, causes, consequences, and solutions

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Conflict of Interest Statement

Authors Molvar and Anderson are employed by Western Watersheds Project, a conservation nonprofit that works to restore native ecosystems, and study the ecological effects of invasive, non-native species, and work to limit the expansion of cheatgrass and restore invaded habitats through addressing human-caused factors leading to its spread, including livestock grazing, mining, and oil and gas development. Authors do not feel that this is a conflicting interest, and evenly present all published perspectives on cheatgrass.

Cover photo: Cheatgrass on the Pole Mountain unit, Medicine Bow National Forest, southeastern Wyoming, by Erik Molvar

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EXECUTIVE SUMMARY

This comprehensive review of a century of scientific inquiry illuminates the causes and consequences of cheatgrass (*Bromus tectorum*) invasions, and evaluates solutions to restore healthy native ecosystems. Introduced to North America in the 1800s, this Eurasian annual was spread by railroads, vehicles, and livestock, colonizing lands disturbed and degraded by overgrazing and other factors. Today, millions of acres have been converted to cheatgrass monoculture. Tens of millions of acres more remain at high risk of invasion. Continuing expansion across vast areas of the West indicates that current livestock grazing remains responsible for cheatgrass expansion and dominance. Cheatgrass is a habitat generalist, has an extremely high reproductive rate, and germinates earlier than native grasses. It outcompetes seedlings of native plants for water and soil nutrients and alters soil chemistry and flora to its own advantage. Livestock trampling, grazing, and surface disturbance are the key ecological switches that transitions healthy arid ecosystems to cheatgrass-invaded systems, by eliminating the native bunchgrasses and biological soil crusts that are the natural defense against weeds. A livestock-cheatgrass-fire cycle now prevails across much of the public lands of the western United States, rendering lands susceptible to larger and more frequent fires. Cheatgrass invasion degrades or eliminates habitat for native wildlife and range for livestock. Climate change will likely shift the distribution of cheatgrass, and may exacerbate invasions. Solutions to restore native habitats remain elusive and expensive. Disking, targeted grazing, prescribed fire, fuelbreak construction risk a worsening of cheatgrass infestations; plantings of non-native forage species create invasive weed infestations of their own; while herbicides, natural parasites, seeding with native plants may fail on the regional scale demanded by the problem. Reduction or elimination of livestock grazing achieves results on a sufficiently large scale, but full restoration can take decades. Conversion of native rangelands to cheatgrass markedly decreases soil carbon, so returning cheatgrass infestations to native plant assemblages could play a key role in climate mitigation. We recommend rest from livestock grazing on an allotment scale until native species replace cheatgrass. On lands with light infestations, we recommend reducing livestock grazing to levels that promote the flourishing of native species and the maintenance of soil biocrusts.

Introduction

Cheatgrass (*Bromus tectorum,* Linnaeus) is the most widespread, and arguably the most problematic, invasive weed in North America. The scientific literature on cheatgrass and related weeds of the genus *Bromus* is voluminous and comprehensive, yet today much of this extensive body of scientific knowledge has been neglected or forgotten. Its species name *tectorum* derives from the growth habit of cheatgrass occupying thatched roofs in its ancestral homelands in Eurasia (Bartlett et al. 2002). This annual grass was named "cheatgrass" because when it invaded

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wheat fields it 'cheated' farmers out of their full harvest (Mack 1981, Knapp 1996). Cheatgrass invasions, at a population density of as little as 10 cheatgrass plants per square foot, result in crop yield reductions of 25 to 31.5% in the Palouse of eastern Washington (Young et al. 1987, Rasmussen 1995, Tepe et al. 2011). Other common names include downy brome, as well as downy chess, early chess, drooping brome, downy cheat, cheatgrass brome, slender chess, downy bromegrass, military grass, bronco grass, Mormon oats, cheatgrass brome, cheat, drooping brome, bromo velloso, wild oats, early chess, and thatch bromegrass (Klemmedson and Smith 1964, Yensen 1981, Thill et al. 1984, Upadhyaya et al. 1986, Mealor et al. 2013).

In *A Sand County Almanac*, Aldo Leopold (1949) lamented the cheatgrass invasions of California, saying,

> "Today the honey-colored hills that flank the northwestern mountains derive their hue not from the rich and useful bunchgrass and wheatgrass which once covered them, but from the inferior cheat which has replaced these native grasses. … The cause of the substitution is overgrazing. When the too-great herds and flocks chewed and trampled the hide off the foothills, something had to cover the raw eroding earth. Cheat did."

Cheatgrass is a winter annual, typically germinating in autumn, overwintering as a basal rosette of leaves, flowering and setting seed in late spring, and dying in midsummer after seed-set; occasionally it has been documented to persist through two winters and the intervening summer when summer moisture is available (Harris 1967, Klemmedson and Smith 1964, Bradford and Lauenroth 2006, Mack 2011). In areas where fires burn frequently, cheatgrass is an early successional species that prevents the re-establishment of native perennial grasses and shrubs (Knapp 1996). Fenesi et al. (2011) found that cheatgrass is a habitat generalist and displays phenotypic plasticity that predisposes it to being highly invasive in the diverse habitats of North America. Hulbert (1955) discussed the relationships between multiple species of *Bromus*, but this analysis will confine itself primarily to cheatgrass (*B. tectorum*) and to a lesser extent red brome (*Bromus rubens*), an ecologically similar annual grass prevalent in the drier, warmer climes of the Mojave Desert.

Other invasive bromes include *Bromus trinii* (Chilean chess), *Bromus arvensis* (Japanese brome or field brome, formerly *B. japonicus*), *Bromus hordeaceus* (soft brome), and *Bromus diandrus* (ripgut brome). Soft brome and ripgut brome occur more in the moister Mediterranean climates of coastal California (Pyke et al. 2016); rip-gut brome does occur in Boise, Idaho and is spreading. Rip-gut is the dominant weedy annual grass in the valleys in Zion National Park (Fertig and Alexander 2009). Japanese brome occurs in moister habitats than does cheatgrass (Hulbert 1955) and is prevalent on the Northern Plains and fringes of the Wyoming Basins ecoregion (Pyke et al. 2016). *Bromus madritensis* (foxtail brome) and *B. rubens* occur from the Mediterranean climates of California to the Mojave Desert (Pyke et al. 2016). *B. madritensis* is the invasive brome most prevalent in central California (Kimball and Schiffman 2003). In hot deserts, *B. rubens* tends to be dominant, with cheatgrass becoming locally dominant at higher elevations, and Chilean chess and compact brome also occurring (Brooks et al. 2016a). In addition to the well-known exotic brome species, there are at least 15 native *Bromus* species that are endemic to North America (Salo 2005).

Medusahead wildrye (*Taeniatherum caput-medusae*) is another invasive winter annual that is unpalatable to herbivores, has injurious awns, and forms dense, fire-prone stands (Hironaka 1994). Medusahead sometimes replaces cheatgrass in the 11-inch and above precipitation zone in the Great Basin (Hironaka 1994). Ventenata (*Ventenata dubia*) is a new invasive annual grass that causes ecological disruption in the intermountain West review of their properties is beyond the scope of this article.

As we discuss below, the causes of cheatgrass expansion are well-understood, and indeed represent a fairly strong scientific consensus, elucidated in an extensive volume of scientific literature spanning almost a century. Livestock grazing is the initial disturbance that suppresses native bunchgrasses and opens the requisite ecological space for a cheatgrass invasion (Klemmedson and Smith 1964, Reisner et al. 2015). Once cheatgrass attains sufficient density in an area as a result of livestock grazing or through

Cheatgrass (purple seedheads) and ripgut brome (lighter seedheads) in southwestern Utah. Matt Lavin photo courtesy Flickr Creative Commons.

other means of disturbance, fires increase in size and frequency, providing positive feedbacks that, with continued disturbance, ultimately lead to a cheatgrass monoculture.

(Jones et al. 2018). While these invasive annuals are emerging as major ecological threats, a detailed

History of a Biological Invasion

The North American cheatgrass invasion is an important example of the worldwide decimation of native flora and fauna by invasive species, which has followed in the wake of the recent introduction of agriculture to areas previously occupied by native ecosystems. Parker et al. (2016:1460) described the consequences of European colonization of North and South America, Australia, and New Zealand as eliminating biotic resistance to plant invasions (native herbivores such as bison, elk, prairie dogs) and replacing it with species that promote further invasions (exotic herbivores, *e.g.*, cattle, pigs, sheep).

Pre-Cheatgrass Ecosystems

Prior to Euro-American contact, North American ecosystems supported robust and diverse assemblages of native plants and animals. In the Intermountain West, Indigenous peoples occupied the landscape, but apart from occasional use of fire, had limited impact on native vegetation communities (Harris 1967). Prior to 1850, the interior West, characterized by winter precipitation, was dominated by perennial grassland and shrubsteppes (Mack 1981, Knapp 1996). Early historical accounts characterize the lower Snake River Plain as being dominated by sparse grasses among the sagebrush, and infrequent fire (Vale 1975, Peters and Bunting

1994). Elsewhere, the Snake River Plain was dominated by sagebrush communities with a rich understory of perennial bunchgrasses, or by winterfat or other salt desert communities (Yensen 1981). Billings (1994) reviewed the early journals of expeditions in the Great Basin and found that uplands were dominated by bunchgrasses from the genera *Festuca*, *Agropyron* (now *Pseudoroegneria*), and *Elymus*. Early pioneers coming into the Salt Lake valley reported grasses six- to twelve-feet tall in the bottoms of Emigration Canyon (Cottam and Evans 1945). In Arizona, a relict grassland never grazed by livestock may represent pristine conditions, and is characterized by a tall growth of diverse native grasses (Ambos et al. 2000), showing what native vegetation might have looked like in that region in the absence of domestic livestock.

In Europe, some large herbivores escaped extinction through domestication; in North America, these largely went extinct. "Therefore, for about 10,000 years prior to the introduction of domestic livestock, there were no requirements for plant species to grow in seral habitats created and maintained by grazing" (Young et al. 1972: 197). In the Great Basin, large herbivores were essentially absent since the Pleistocene (Young and Evans 1978, Mack 1981, Mack and Thompson 1982, Fleischner 1994). Grayson (2006) contended that bison were widespread (but did not address densities) across northern Utah and Nevada and into southeastern Oregon starting during the very late Holocene (mostly after 400 A.D.), and largely disappeared by 1400 A.D. due to climactic shifts (*see also* Lupo and Schmitt 1997). Arid and semi-arid ecosystems in North America west of the Continental Divide are poorly adapted to heavy herbivore grazing, because bison were sparse and patchy to absent in this region during pre-settlement times (Kaczmarski 2000, Carter et al. 2014). Bison would have been present at low densities in the upper (eastern) Snake River Basin, but largely absent from the lower Snake River Plain (Peters and Bunting 1994, and see Henrikson 2004). Because intermountain shrubsteppe evolved with lighter, more intermittent grazing by large herbivores, when heavy cattle grazing was introduced, grazing-intolerant native grasses were replaced by invasive weeds (Milchunas et al. 1982).

The historical disturbance regime of Wyoming big sagebrush shrubsteppe consisted of periodic fires with minimal grazing by large herbivores (Davies et al. 2009). Fire return intervals in Wyoming big sagebrush under natural conditions were 100-240 years (Baker 2007). Fire was not considered part of salt-desert scrub communities prior to 1983, but changing climate and a profusion of cheatgrass has made fire a frequent (if unnatural) event in these plant communities (West 1994).

While the intermountain basins, where ungulates were less common, are characterized by grazing-intolerant bunchgrasses and biological soil crusts, the Great Plains, where herbivores were abundant during pre-settlement times, are characterized by more grazing-resistant, sod-forming grasses (Mack and Thompson 1982, Milchunas et al. 1988, Warren and Eldridge 2001). In contrast to the Great Basin, the Great Plains receives a greater proportion of its annual precipitation during summer, when perennial grasses are active, and when fire season is at its peak (Porensky and Blumenthal 2016). Perennial grasses in the intermountain basins, by contrast, evolved to commence their growth early and complete their growth by midsummer, in order to escape the summer droughts brought on by prevailing westerly winds that have been a hallmark of Intermountain West since the Pliocene epoch (Mack and Thompson 1982). Noting the lack of severe cheatgrass invasions on the Great Plains, Bradford and Lauenroth (2006) concluded that cheatgrass outcompetes native plants in areas with consistent winter precipitation and moisture availability. Patagonian steppes, also coevolved with generalist herbivores, are more resistant to grazing than North American sagebrush steppe (Adler et al. 2005). Bradford and Lauenroth (2006) attributed the lack of large-scale cheatgrass invasions in Patagonian steppe largely to differences in disturbance regime, as climactic suitability is similar to North American sagebrush ecosystems.

Vale (1975) reviewed 29 historical journals and diaries from the pre-livestock era, and determined that sagebrush basins were heavily dominated by shrubs during pre-settlement times, with pure swards of grass confined to wet valley bottom areas. Johnson (1986: 231) compared photographs taken in the 1870s with corresponding photographs from the 1970s and concluded, "While it is clear that changes in sagebrush density have occurred, it is equally clear that there has been no major shift in sagebrush distribution as a result of [livestock] use." In the Columbia Basin, cheatgrass encountered growing conditions most conducive to its establishment and spread (Harris 1967). Mack and Thompson (1982) hypothesized that the relative absence of bison in the Great Basin and Columbia Basin is due to the fact that perennial bunchgrasses aestivate throughout most of the summer, losing nutritional quality at a time when large herbivores face the maximum nutritional demand imposed by lactation to support rapidly-growing offspring.

According to Knapp (1996), "Collectively, the impact of native Great Basin animals was light and rarely damaging. This was essential, since C4 sod-forming grasses, such as grama and buffalo grass, which can support heavy grazing and protect the soil, were uncommon in the Great Basin. Instead, C3 bunchgrasses (that evolved without heavy grazing) separated by fragile cryptogamic crusts were the norm." According to Olff and Ritchie (1998: 263-4),

> "Dry environments on infertile soils have low productivity and favor plants that compete well for both nutrients and water in the absence of herbivory (e.g. in deserts). … Such a plant community may, therefore, support a few, small herbivores, and these herbivores are likely to select rare, palatable species. Hence, they will have little effect on plant competition and consequently induce few plant coexistence mechanisms. Therefore, herbivory could increase extinction rates. … Low natural abundance of herbivores implies that few plants in the species pool have evolved a tolerance to grazing. Introductions of high densities of large mammalian grazers that were supplementary fed, such as livestock, are therefore likely to reduce [plant] diversity dramatically."

The intolerance of native plants to grazing by large herbivores would set the stage for cheatgrass invasion once domestic livestock became widespread in the region.

Eurasian Origins of an Invasive Weed

The Mediterranean region of Europe, where agricultural activity has created soil disturbances for millennia, has a large and successful assemblage of weedy species (Hobbs and Huenneke 1992). Among these, cheatgrass is widespread across Eurasia, but rarely becomes a community dominant except in Central Asia states like Turkmenistan and Uzbekistan (Mack 2011). Humanity's domestication of livestock in Eurasia created an early-seral niche through concentrated overgrazing, and a series of Eurasian annual plants including cheatgrass evolved to exploit this niche (Young et al. 1972, Terpó et al. 1999). Nomadic herding tribes of central Asia propagated annual grass communities through long-term or repeated concentrations of grazing livestock along their migratory routes (Young et al. 1972). In Old World settings, red brome is prevalent in desert shrublands where biological soil crusts have been disturbed (Zaady et al. 2003). In Europe, where cheatgrass is native, *B. tectorum* actually suffered from disturbance caused by livestock, but benefitted from livestock feces (Eichberg et al. 2007). Fenesi et al. (2011) found that cheatgrass in its native habitat occurred in both disturbed areas and in semi-natural areas, co-occurring with native habitat-specialist species. However, Mack and Thompson (1982: 763) observed that the long-term dominance of plant communities by cheatgrass is a uniquely North American phenomenon. Central Asian grasses had a much stronger competitive effect on cheatgrass than did North American grasses, which explains in part why cheatgrass is a minor component in its home range but dominates in North America (He et al. 2011). The eastern Mediterranean has been grazed by domestic livestock for 5,000 years, and grasses that decrease in the face of sustained grazing may already have been eliminated, while the Great Basin has been grazed by livestock for only 130 years, and native grasses are heavily skewed toward decreasers (Condon and Pyke 2018).

Based on genetic analyses, the source population for cheatgrass in the eastern United States was likely either Afghanistan or central Europe (Bartlett et al. 2002). Novak and Mack (2001) concluded based on genetic analyses that North American cheatgrass populations derived exclusively from western and central Europe, but left room for the possibility that Afghanistan cheatgrass varieties could have been transported to western Europe prior to being transported to North America. Genetic markers prevalent in cheatgrass populations in the Midwestern states have been linked to Vaç, Hungary and Bratislava, Slovakia (Huttanus et al. 2011). A form of cheatgrass originating between Beyreuth, Germany and Prague dominate the United States west of the Rocky Mountains, based on genetic markers (Valliant et al. 2007, Mack 2011), while the eastern Canadian cheatgrass population has been linked to eastern Europe (Vac, Hungary and Bratislava, Slovakia, Valliant et al. 2007).

Cheatgrass Arrives in North America

The earliest record of cheatgrass in North America was made in Lancaster County, Pennsylvania in 1790 (Bartlett et al. 2002). Eastern populations arose from at least two introduction events, while there was at least one separate introduction event on the West Coast (Bartlett et al. 2002). Cheatgrass introduced to the Midwest came either directly from Europe, via slow westward spread from eastern populations, or through commercial shipping via the Great Lakes (Huttanus et al. 2011). Novak and Mack (2001: 118) asserted that eastern and western cheatgrass introductions were not related, but that western populations are derived from additional immigration events and have a mosaic of genotypes.

Cheatgrass was collected in New York prior to 1861 (Klemmedson and Smith 1964). The first recorded cheatgrass herbarium specimens are from Pennsylvania in 1861, supplemented in Washington in 1893, Utah in 1894, Colorado in 1895, and Wyoming in 1900 (Stewart and Hull 1949, Klemmedson and Smith 1964). It had spread to every state by 1914 (Stewart and Hull 1949). The first Canadian specimen of cheatgrass was collected in 1886 in Kingston, Ontario; introduction on the Canadian west coast occurred three years later (Vaillant et al. 2007). Early transport throughout Canada was via railroad, while early specimens along Great Lakes provinces are all from ports, suggesting transport by boat or ship (Vaillant et al. 2007). Influxes of Mormon settlers from Utah between 1886 and 1905 brought cheatgrass to southern Alberta, supplemented by shipments from the U.S. of cheatgrass-dominated hay during the winter of 1919-20 in "one of the best-documented cases of *B. tectorum* dispersal along paths of human migration" (Vaillant et al. 2007: 1167). Cheatgrass now occurs in all Canadian provinces, from New Brunswick and Nova Scotia to British Columbia, and northward to Yukon (Upadhyaya et al. 1986). Cheatgrass invasions have also occurred in Argentina, Chile, the Canary Islands, New Zealand, and Hawai'i (Novak and Mack 2001).

Cheatgrass Spreads

Between 1850 and 1870, gold and silver discoveries in the mountains bordering sagebrush basins led to an influx of cattle, accompanied by local overgrazing (Mack 1981). Beginning in 1864 cattle by the thousands were brought to the area near Virginia City, Nevada to support mining activities; by the 1850s sheep were present and damaging ranges in the Great Basin (Knapp 1996). Enormous numbers of cattle and sheep between 1870 and 1930 caused major degradation of western rangelands (Miller and Eddleman 2000). From 1880 to about 1910, abusive grazing accompanied by burning resulted in a massive reduction in native perennial grasses and a reduction of the carrying capacity for livestock of nearly 50% (Yensen 1981, citing Pickford 1932). There were about 1.2 million sheep in Nevada by 1908, and wild horses numbered 100,000 at the turn of the 20th Century (Knapp 1996). Cattle were generally confined to lowlands and gentle slopes, while domestic sheep traveled into steeper country and high mountain meadows (Knapp 1996). Heavy livestock grazing in the 1800s removed fine fuels and may have reduced the number of fires and the acres burned (Launchbaugh et al. 2008).

Cheatgrass began to appear in adulterated grains in the 1880s with homesteading and farming in the Columbia Basin (Mack et al. 1981, Knapp 1996). Initiation of cheatgrass invasion in interior British Columbia suggests that it arrived as a wheat contaminant (Upadhyaya et al. 1986). Field plowing for winter wheat coincides with the optimum time for cheatgrass spread, and widespread adoption of winter wheat helped spread the cheatgrass invasion (Mack 1981). Ultimately, steam-powered grain threshers moving from farm to farm likely moved cheatgrass among agricultural lands (Young and Allen 1997: 531).

The spread of invasive species is typically modeled as a steady expansion, but may also be radically altered by rare events involving long-distance transport of seeds (Hastings et al. 2005).

Cheatgrass seeds were then spread along railways in livestock dung and bedding straw (Mack 1981). Yensen (1981) recorded accounts of cheatgrass being fed to sheep traveling via railway cars, and postulated this as the origin of cheatgrass invading native vegetation within 300 feet on either side of railroad tracks. In Saskatchewan, introduction of cheatgrass likely occurred with the transport of contaminated hay, winter wheat seed, and forage seed into and throughout the region (Douglas et al. 1990). Cheatgrass was then spread by flocks driven by Basque sheepherders, in all likelihood, and frequent fires caused by steam locomotives and brake sparks along railroad rights-of-way likely facilitated its spread (Young and Allen 1997).

Klemmedson and Smith (1964) hypothesized that abandoned farmlands provided the first sites of large-scale cheatgrass invasion, and from there cheatgrass spread to rangelands subject to overgrazing and other disturbances. Cheatgrass expanded rapidly into rangelands that had been badly overgrazed by the 1890s, and by the turn of the 20th Century, the native perennial bunchgrasses were essentially destroyed across large areas (Mack 1981). Young et al. (1972) argued that by the turn of the 20th Century, heavy livestock grazing had severely degraded perennial grasses, but invasive annuals remained rare to absent; cheatgrass distribution at this time was small and confined to local populations. In southwestern Idaho, as sagebrush increased in density due to this overgrazing of bunchgrasses, large areas were burned by stockmen to stimulate grass production for their livestock (Quinney 2000). In some cases, overgrazed lands were seeded by agricultural experiment programs and seed sellers in an effort to revegetate rangelands denuded by cattle and sheep (Mack 1981). This was followed by cheatgrass invasion and monoculture establishment.

Intense, year-round grazing contributed to the loss of native perennial grass cover and the loss of soil (Stromberg et al. 2007). There was a rapid spread of cheatgrass across much of North America between 1880 and 1900, including mid-American locales like Fort Collins, Colorado and Ames, Iowa (Mack 2011). Cheatgrass was collected in 1895 in Colorado by C.S. Crandall and in 1900 by Aven Nelson (Warg 1938). Cheatgrass was first reported in Provo, UT in 1894, in Elko, NV in 1905, and in Reno, NV in 1906 (Knapp 1996); and in Elko County NV in 1906 (Young et al. 1987). About 1915, cheatgrass began to colonize overgrazed rangelands in Idaho (Young and Allen 1997). Yensen (1981) postulated that the first cheatgrass in Idaho may have arrived from seeds carried in the pelage of domestic sheep trailed in from California through Nevada. What Yensen (1981) termed "abusive grazing and burning" allowed cheatgrass to become the dominant plant on millions of acres in southern Idaho. Other types of domestic livestock and wild horses further disseminated cheatgrass (Knapp 1996).

After 1890, cheatgrass spread in two major tongues, one in the Northern Plains and one in the Southern Plains (Mack 2011). Stewart and Young (1939) placed the major expansion of cheatgrass a bit later, and emphasized invasion on degraded sites. By 1903, range condition in northeastern Nevada varied from overgrazed at lower elevations to virtually pristine on some mountain slopes, but without reports of cheatgrass; by 1953, perennial grasses were suppressed and cheatgrass increased to an extreme degree in this region, with heavy cover across much of the landscape (Robertson and Kennedy 1954).

The livestock industry and its promoters actively, and in some cases intentionally, advocated for the planting of cheatgrass before it became widely recognized as an undesirable weed. "Cheatgrass was found to provide good forage in the early spring, and many ranchers intentionally burned sagebrush rangeland to increase this forage source," observed Peters and Bunting (1994: 33, internal citations omitted). Ranchers commonly used fire to rid their range of sagebrush (Blaisdell 1953). Yensen (1981: 177) agreed, stating, "many stockmen, erroneously believing that burning the shrublands produced good stands of grasses even when grazing pressure following burning was not reduced, deliberately set range fires" (internal citations omitted). Prescribed fires in Kings Canyon National Park, which historically had sheep drives, assisted cheatgrass in expanding from roadside and trailside areas into surrounding ponderosa pine (*Pinus ponderosa*) woodlands (Keeley and McGinness 2007).

According to Young and Allen (1997), conversion from native vegetation to cheatgrass accelerated during the 20th century. According to

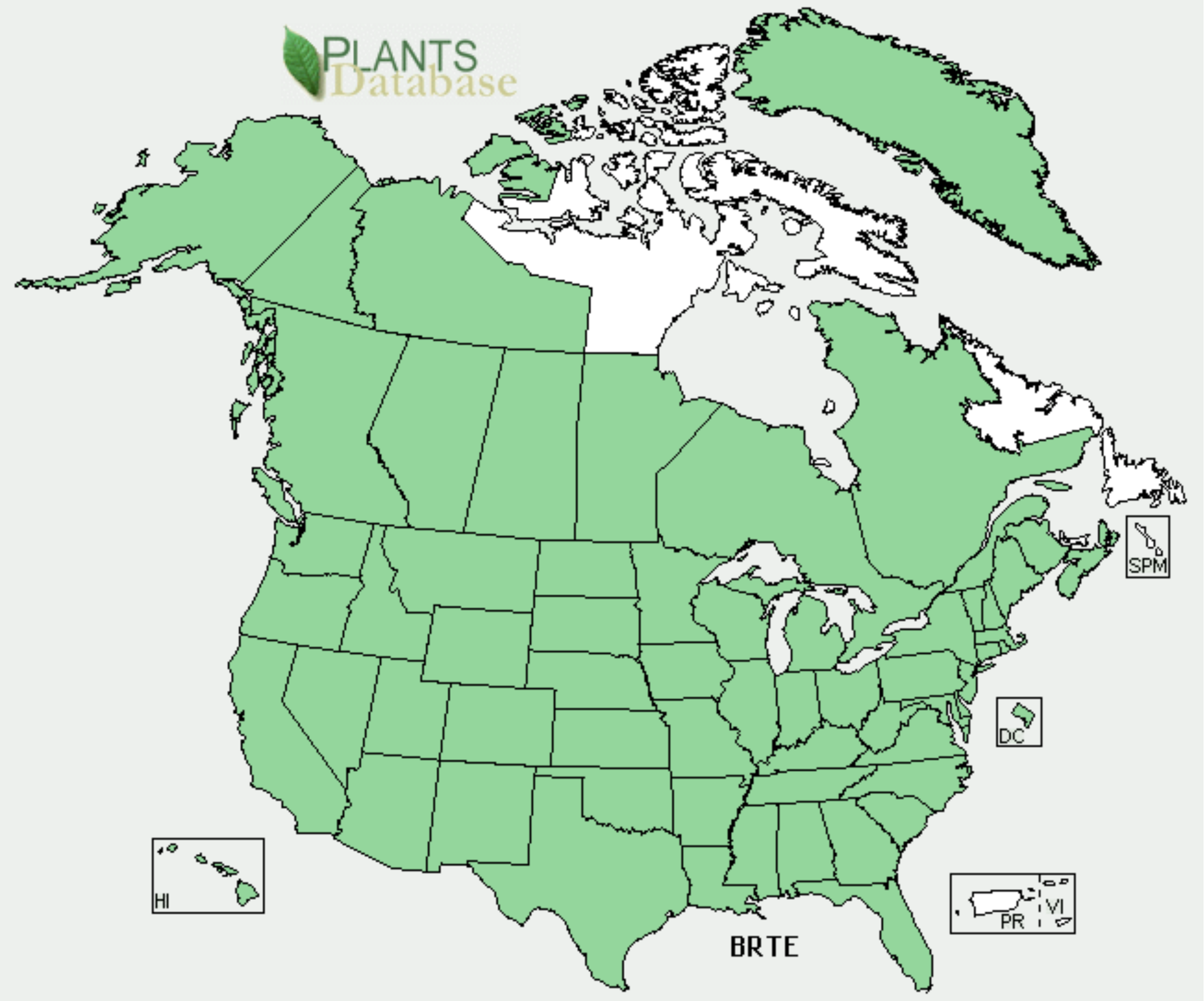


Figure 1. Cheatgrass distribution in the United States and Canada. Reproduced from USDA Natural Resources Conservation Service PLANTS database.

Yensen (1981: 177), continuous burning and overgrazing greatly damaged native grass, sagebrush and winterfat populations. Starting during World War I, cheatgrass infestations in alfalfa fields became severe and widespread (Mack 1981). Abandonment of crop fields after World War I may have contributed to further cheatgrass spread (Stewart and Hull 1949, Young et al. 1987, Young and Allen 1997). Thill et al. (1984) contended that the range of cheatgrass had reached its contemporaneous extent (see Figure 1) by 1928.

By the 1930s, heavy grazing had facilitated the cheatgrass spread throughout the Great Basin (Mack 1981), and large fires in cheatgrass-invaded rangelands became common (Billings 1994). By 1932, spring and fall ranges in Utah had become so damaged by overgrazing that a serious shortage of spring and fall forage resulted (Pickford 1932). It was a combination ideal for cheatgrass spread. Even so, there were areas where cheatgrass presence was sparse. In Utah, as of 1932, cheatgrass was limited to the area between American Fork and Snowville between the Wasatch Mountains and the Great Salt Lake (Pickford 1932). The effect of drought on already-degraded western ranges in the 1930s was extreme (Young and Allen 1997). During the Dust Bowl years, the drought of 1934, combined with heavy and "abusive" livestock grazing, took a heavy toll on sagebrush-bunchgrass communities (Young and Allen 1997). The excesses helped hasten the end of the uncontrolled grazing on federal lands culminating in the Taylor Grazing Act, which was (at least in part) intended to end the damage to public lands (Knapp 1996).

During the Great Depression, Civilian Conservation Corps teams attempted to reseed degraded sagebrush rangelands with programs that included mechanical destruction of sagebrush itself (Young and McKenzie 1982). Wheatland plows were used for sagebrush eradication in the 1930s, but experienced frequent breakage on rough or rocky terrain; in 1947, the brushland plow was brought to the western U.S. from Australia, with independently-suspended disks that were more resilient on rough terrain (Young and McKenzie 1982). There are few records to support the relative effectiveness or futility of these efforts, but the continued expansion of cheatgrass through the 20th Century speaks to the result that the cheatgrass problem was not overcome. By the 1950s, Hulbert (1955) observed cheatgrass at every location visited from eastern Washington and Oregon to northeastern Montana, often as the dominant ground cover.

During these years, agricultural interests began a program of introducing foreign grass species they found desirable, partly to combat cheatgrass, partly to revegetate degraded lands, and partly to sustain more domestic livestock on western rangelands. Crested wheatgrass (*Agropyron cristatum*) was first transplanted to the United States from Russia in 1898, and ultimately became the most heavily-used introduced grass in the western United States (Rogler and Lorenz 1983). Cultivation of crested wheatgrass in North America was first attempted in 1906 (Rogler and Lorenz 1983), and the first major crested wheatgrass seeding project took place in 1936, spanning 57,000 acres in the Curlew and Black Pine Valleys in Idaho (Young and McKenzie 1982). Crested wheatgrass plantings became widespread during World War II to revegetate rangelands denuded during the Dust Bowl (Jones 2000). Mechanical and chemical manipulations of western rangelands began in the 1940s, with a great deal of conversion to crested wheatgrass, peaking in the 1950s and 1960s (Miller and Eddleman 2001). Following large-scale die-offs of domestic sheep in 1947 as a result of halogeton poisoning, a federal law was passed in 1952 funding a further expansion of large-scale crested wheatgrass plantings (Jones 2000). Blaisdell (1953: 2) is representative of the prevailing attitudes of this period, claiming that big sagebrush was "a definite obstacle to range improvement." Large-scale sagebrush removal, through disking and chaining, was also prevalent during this period. BLM undertook sagebrush eradication across 4.5 million acres between 1940 and 1994 (Miller and Eddleman 2001). As of the mid-1970s, crested wheatgrass was established on 14.4 million acres in the United States and Canada. In Nevada, about 1 million acres of sagebrush rangelands were planted to crested wheatgrass; this 2% of the available rangeland produced 10% of the livestock animal unit months in the region (Young and McKenzie 1982). According to Young et al. (1987: 267), "Over a million acres of the 29 million acres of degraded big sagebrush communities in Nevada have been converted to crested wheatgrass."

Despite the Taylor Grazing Act, livestock grazing on public land was largely unmanaged until the late 1960s, and during this period native bunchgrasses were lost due to overgrazing across much of the West (Pyke et al. 2016). Young et al. (1972: 195) characterized the ecological transition during this agriculture-dominated period as first pristine, then exploited by grazing and fire, and finally attempted complete fire suppression. Each of these strategies facilitated the spread of cheatgrass. But it would be the land management practices of the 50 years that followed that resulted in the greatest spread of cheatgrass, and the unprecedented range fires that accompanied that expansion. As of 2011, cheatgrass occurred in all U.S. States except Florida (Mack 2011).

Red brome is the most prevalent invasive *Bromus* species in the Mojave Desert (Brooks and Berry 2006), and its invasion timeline parallels that of cheatgrass. The earliest collection of red bromes was in 1879, from Plumas County, California (Salo 2005). Red brome ultimately spread from British Columbia to Mexico, assisted by the gold rush, wheat cultivation in California's Central Valley, shipping in southern California, and/or domestic sheep in northern California (Salo 2005, Reid et al. 2008). Early collections of red bromes are concentrated in California's Central Valley, but by 1920, red brome was also common along California's Pacific coast (Salo 2005). Salo (2005) attributed the greatest periods of red brome spread, 1930-1952 and 1955-2005, to El Niño Pacific Decadal Oscillation events linked to increased winter precipitation.

The plant communities of the Mojave Desert likewise did not evolve with large herbivores, and

Above: *Desert scrub invaded by red brome in an area of Gold Butte National Monument in southeastern Nevada, an area continuously grazed by cattle. This demonstrates the continuous nature of fine fuels that occurs as a result of red brome invasion.* ***Below:*** *A neighboring area of Gold Butte N.M. that burned in 2005, substantially fueled by red brome invasion.*

its plants are not well-adapted to grazing pressure (Pendleton et al. 2013). *Bromus rubens* invaded the Mojave Desert in the 1920s, initially spreading on disturbed areas (Hunter 1991). Cheatgrass is also present, but at low densities, in the Mojave Desert (Brooks and Berry 2006), and can be locally dominant following fire (Brooks and Matchett 2003). *Bromus tectorum* was first collected in the Charleston Mountains of Nevada in the 1930s, and began spreading to the Mojave Desert during the 1950s, becoming common below 5,000 feet elevation in the 1980s (Hunter 1991). Fire frequency was historically low in creosote bush and saltbush deserts of the Mojave, and the invasion of annual grasses increased fire frequency (Brooks and Pyke 2002). Smith et al. (2023b) found that hotspots for annual grass invasion were concentrated along the eastern and western margins of the Mojave Desert.

Magnitude of the Ecological Destruction

Anderson and Inouye (2001) asserted that sagebrush steppe as an ecosystem is endangered by losses to agriculture, excessive livestock grazing, and invasive species. Wisdom et al. (2005) identified more than 350 species of sagebrush-associated plants and animals of conservation concern within the historical range of the greater and Gunnison sage-grouse. Some native bunchgrasses have disappeared almost entirely in the face of sustained grazing pressure by livestock (*see, e.g.,* DeFlon 1986). Garner et al. (2019: 91) noted that a reduction in native plants with simultaneous increase in invasive plants reduces ecosystem resiliency and its ability to recover after fire. The net effect of conversion of native sagebrush steppe to cheatgrass monoculture has been to increase the aridity of the region (Chambers and Wisdom 2009).

Worldwide, invasive plants constitute "a major threat to biodiversity" (Vavra et al. 2007: 66). Wilcove et al. (1998) ranked alien species second only to habitat destruction and degradation as a threat to imperiled species in the United States. Almost half of federally threatened and endangered species, perhaps most notably the desert tortoise, are listed in part due to threats from invasive species and fire (Brooks and Pyke 2002). Garner et al. (2019: 90) asserted that invasive annual grasses including cheatgrass are arguably the most widespread disruptors in sagebrush habitats. Peters and Bunting (1994: 31) agreed, asserting that annual invasive grass invasion of the Snake River Plain is likely the most significant ecological event since the end of the last ice age. Even relatively moderate expansions of biological invasions are expected to have a disproportionately heavy impact on biodiversity (Essl et al. 2020). According to Wisdom et al. (2005: 6, references omitted), "Invasion of exotic vegetation, altered fire regimes, road development and use, mining, energy development, climate change, encroachment of pinyon-juniper woodlands, intensive grazing by livestock, and conversion to agriculture, to urban use, and to non-native livestock forage all have contributed to the [sagebrush] ecosystem's demise."

Cheatgrass invasions not only imperil wildlife, but the diversity of native plants as well. Cheatgrass typically attains dominance following fire and/or grazing, and this can lead to a weed monoculture devoid of vegetative diversity (Germino et al. 2016). Vegetation distribution becomes progressively less heterogeneous with cheatgrass invasion (Ceradini and Chalfoun 2017). Cheatgrass can form an almost continuous understory in sagebrush communities (*e.g.,* Rice and Westoby 1978), and their seeds come to dominate the seedbank of such degraded big sagebrush communities (Young and Evans 1975). Sagebrush with an understory of annual grasses then becomes extremely vulnerable to transition to annual grassland as a result of fire (Sands et al. 1999). In California grasslands, livestock grazing reduces native plant diversity, eliminating some native plants entirely (Kimball and Schiffman 2003). Peters and Bunting (1994: 31) linked cheatgrass invasion, fire cycles, and domestic livestock grazing with inexorable changes to vegetation species composition, physiognomy, and function. Thus, in less than 120 years, *B. tectorum* has transformed much of the grasslands from central Nevada to southern British Columbia; native regional communities persist only on tiny protected land parcels (Daubenmire 1970), and even these sites are "under constant threat from the cheatgrass juggernaut."

The interior Columbia Basin and lower Snake River Plain have the most widespread, heavy infestations of cheatgrass in North America (Bradley et al. 2018). Upadhyaya et al. (1986: 692) remarked, "In some cases, the vegetation on overgrazed rangeland consists totally of downy brome." In the Great Basin, cheatgrass replaced millions of hectares of native shrub and bunchgrass communities (Whisenant 1990). A large fraction of the cold desert shrublands in the Interior West are in severely degraded condition, and dominated by weedy annual grasses that turn them into carbon sources rather than carbon sinks (Meyer 2012).

Areas substantially invaded by cheatgrass now span tens of millions of acres. Knapp (1996: 37) observed that approximately 20% of the sagebrush-steppe vegetation zone is dominated by cheatgrass to the point where the establishment of native perennial species is nearly impossible. For the central Great Basin, Balch et al. (2013) put this figure at not less than 6%. As of 2005, cheatgrass extent had reached 7,000,000 hectares (17.3 million acres, Belnap et al. 2005). The same year, Bradley and Mustard (2005) estimated that 20,000 km^2 (or 4.9 million acres) showed signals of outright cheatgrass dominance. By 2009, cheatgrass covered at least 51 million acres in the West, about 39% of the Great Basin (Epanchin-Neill et al. 2009); Rowe et al. (2009) estimated the acreage of cheatgrass-infested lands in the United States at 99 million acres that same year. Mealor (2013) reported that cheatgrass infested more than 101 million acres at the time of publication. High-density cheatgrass infestations continue to worsen over time. Cheatgrass cover exceeds 15% across 51.9 million acres (210,000 km^2), nearly one-third of the Great Basin (Bradley et al. 2017, 2018, see Figure 2). Ricca and Coates (2020) mapped 19 million acres of recent fires in the Great Basin (Figure 3), and based on GIS analysis of their data, classified 4,732,780 acres (25%) as recovered, 4,579,810 acres (24%) as recovering, and 9,688,700 acres (51%) as having already transitioned to cheatgrass monoculture.

The problem is likely to get worse as cheatgrass continues to expand in both extent and dominance. As of 1994, cheatgrass was dominant across 3.3 million acres of public land in the Great Basin, and another 71.6 million acres was either infested with cheatgrass or susceptible to invasion (Pellant 1996). Almost 80% of the land area in the Great Basin was considered to be at some risk of displacement by cheatgrass in 2005, of which 65% was found to be at moderate to high risk (Suring et al. 2005). Figure 4, reproduced from Wisdom et al. (2005) shows risk of cheatgrass displacement of sagebrush in Nevada over a 30-year period. Salt desert scrub covers 25% of the Great Basin, and in this habitat type nearly 80% (5.8 million ha) was estimated to be at high risk of displacement by cheatgrass (id.). Almost 38% of sagebrush habitats were at moderate risk of displacement and almost 20% were at high risk. In the Great Basin, an additional 100,000 km^2 of sagebrush steppe and 50,000 km^2 of dry desert shrub communities are at high risk of conversion to cheatgrass (Bradley et al. 2006), adding up to 37 million acres of cheatgrass monoculture. In a newer analysis under extant climate conditions, Bradley (2009) reported that almost 188 million acres are susceptible to future cheatgrass invasion in the western United States.

Bradley and Mustard (2005) argued that northern Nevada, western Utah, and Harney County, southeast Oregon had the most severe invasions of cheatgrass. As of 1998, there were 17.5 million acres in Utah and Idaho infested with cheatgrass (Westbrooks 1998). In Grand Staircase – Escalante National Monument (on the Colorado Plateau), cheatgrass comprised 68% of the exotic plant species cover (Stohlgren et al. 2001, Bashkin et al. 2003), and Chong et al. (2006) found that cheatgrass cover in this area was as great as cover of any single native plant species.

Boyte and Wylie (2016) found an overall mean cheatgrass cover percentage for the northern Great Basin of 9.85%, with concentrations above 60% along the lower Snake River Plain. The Snake River Plain was the epicenter for recurrent fires on the same habitats (Brooks et al. 2015). Fuel conditions outside of the natural range can result in changes in fire behavior and fire regime, which may result in local extirpation for species that cannot persist under the new fire regime (Brooks et al. 2004). Of shadscale-dominated salt-desert ecosystems in the Great Basin, Meyer et al. (2001: 224) reported that these ecosystems have been heavily impacted by livestock grazing and weed invasion over the past century and a half, and few if any truly pristine areas remain. The Wyoming Basins are relatively rich in native grasses, and experienced a mild level of cheatgrass invasion relative to other regions (Reid et al. 2008). Porensky and Blumenthal (2016) found cheatgrass cover greater than 40% on the Thunder Basin National Grassland, on the Great Plains. According to Young and Clements (2007: 16), "The profession of range management

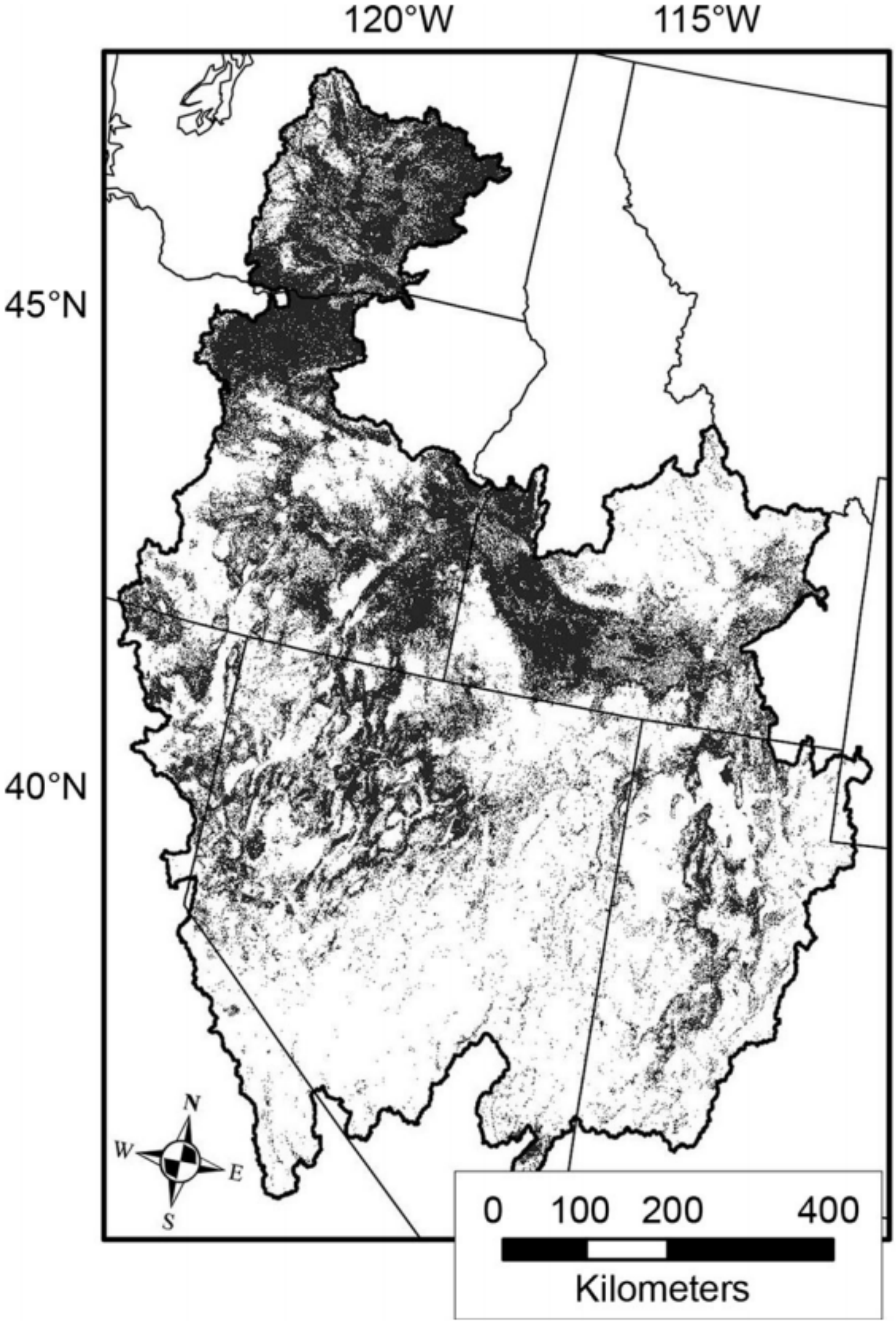


Figure 2. Distribution map of abundant cheatgrass presence (at least 15% cover; gray areas), reproduced from Bradley et al. (2018).

has been deeply involved in an imitation of the Roman Emperor Nero, but in this case they 'fiddle' while the ranges of the Intermountain Area of Western North America burn."

Why Cheatgrass is a Potent Invader

Native ecosystems of North America evolved in the absence of cheatgrass, in the absence of frequent fires, and in many cases in the absence of numerous large herbivores. Into this environment ill-adapted to resist its incursions, cheatgrass arrived with a host of ecological advantages. Disturbances brought by Euro-American settlement granted further advantage to the expanding weed. Warg (1938: 22) observed cheatgrass to be most dominant in abandoned fields and on overgrazed and burned areas. Likewise, red brome, with its greater root surface area and superior ability to exploit deep soils, can take advantage of greater ability to access soil water and nitrogen in hot deserts to outcompete native annuals (DeFalco et al. 2003). Because invasive species have short generation times, high fecundity, strong seed dispersal ability, broad environmental tolerances, and rapid growth, global climate change favors invasive species over native species (Bradley et al. 2010).

Cheatgrass has a few main roots (an average of seven); and a finely divided fibrous root system that reaches approximately 30 cm deep, with depths up to 150 cm; and a dense, shallow root system (Upadhyaya et al. 1986). Cheatgrass has a high density of very fine roots in the uppermost soil horizon, 83% more fine roots than is found in native shrub steppe (Norton et al. 2004). The roots of cheatgrass are small and fragile, in contrast with the roots of native bunchgrasses, which are robust (Hulbert 1955, and see Klemmedson and Smith 1964). Cheatgrass has a greater root biomass, length, and surface area, and a greater root-to-shoot ratio, than native perennial grass when grown from seedlings, which explains its greater competitiveness for nutrients (Vasquez et al. 2008). *Bromus* roots can reach 2m in depth in the soil, but most roots are concentrated in the top 20-30cm (Chambers et al. 2016). Maximum observed depth of cheatgrass roots reported by Harris (1967) was 1.17m. Once the roots of perennial grasses penetrate below 0.5m (19.7 in.) depth, they become relatively free from competition with cheatgrass roots (Carpenter and Murray 2005). This requires perennial grasses to mature to the point at which they produce deep roots, which is difficult in the presence of cheatgrass competition. Cheatgrass can coexist with deep-rooted shrubs and forbs, which do not compete as directly with cheatgrass for moisture and nutrients at the upper horizons of the soil (Chambers et al. 2016).

Cheatgrass is a major impediment to bunchgrass seedling establishment (Nelson et al. 1970). Native perennial seedlings establish successfully where cheatgrass plant density is less than 300 plants per meter (Mazzola 2008). This may be a critical threshold beyond which native bunchgrasses cannot become established from seed. For reference, a study in southern Idaho showed a cheatgrass density ranging from 100 to 1,400 cheatgrass plants per square foot (1,076 to 15,069 plants per square meter), with an average density of 6,157 plants per square meter (Stewart and Hull 1949).

Cheatgrass expands so rapidly because it is a prolific seed producer, can germinate in spring and autumn giving it a competitive advantage over native grasses, is tolerant of grazing, and increases with fires (Pellant 1996). Its sharp awns defend cheatgrass against herbivory (Mealor et al. 2013) by native wildlife and domestic livestock alike. Because of the "double jeopardy" of superior competition for soil nutrients and increasing fire frequency, it is extremely difficult to re-establish perennial grasses once cheatgrass attains dominance on a site (Cox and Anderson 2004).

Cheatgrass thrives where the native plant cover has been killed or badly damaged (Stewart and Hull 1949). The pattern of cheatgrass invasion is initial introduction, followed by spread following disturbance (typically livestock trampling or industrial development), followed by understory dominance in response to grazing, followed by fire and conversion to cheatgrass monoculture. Seven study sites scattered from eastern Washington to west-central Utah had intact sagebrush overstories, but annual grass cover ranging from 0-50% areal cover (Rau et al. 2011). Cheatgrass dominance in the understory can last 20 years or more (Goodwin 1992).

Cheatgrass appears to be able to grow across a broad spectrum of soil temperature, nutrient, and moisture levels. Warmer soil temperatures following vegetation treatment projects can result

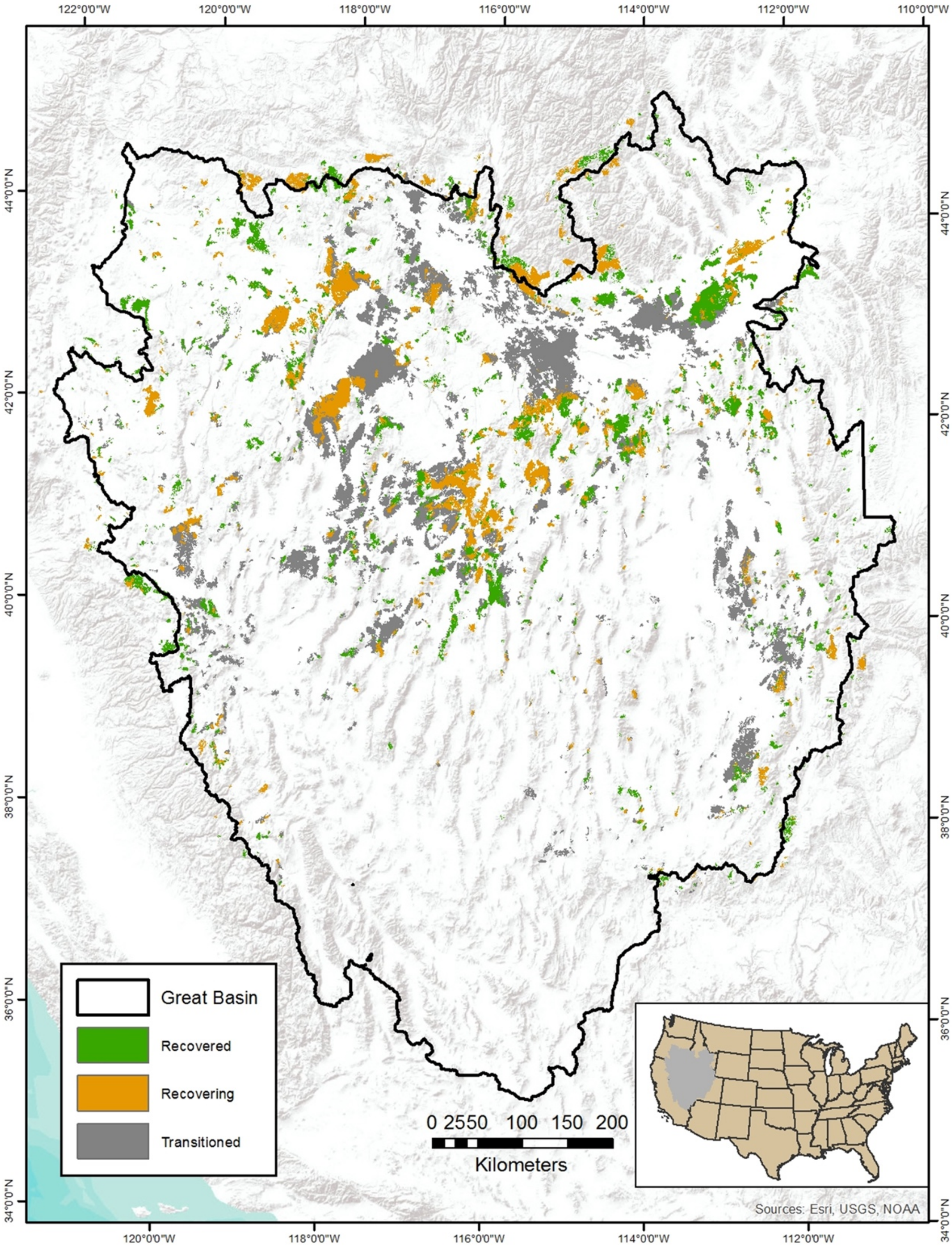


Figure 3. Burned lands in the Great Basin as fully recovered, recovering from fire, or transitioned to cheatgrass monoculture. Reproduced from Ricca and Coates (2020).

in increased cheatgrass growth, but also increased perennial grass growth (Roundy et al. 2018). Rising soil temperatures were the best correlate to cessation of plant growth in cheatgrass; growth ceased at 27°C (Uresk et al. 1979). Pulses of recruitment of cheatgrass seedlings in autumn followed periods of precipitation in both steppe and forest environments (Rice and Mack 1991).

Bradley (2009) created a bioclimactic model for cheatgrass, and projected that a lack of summer precipitation was the best predictor of cheatgrass presence. Spring precipitation may also be key to cheatgrass productivity (DeFlon 1986). Wet winters create moist spring soil conditions that increase the probability of cheatgrass establishment (Bradford and Lauenroth 2006).

An Adaptable Generalist

Invasive weeds can be more successful by having a genetic predisposition to being generalists, surviving in a broad array of habitats and circumstances, and/or by having the ability to rapidly take advantage of surges in available resources through being superior competitors (Richards et al. 2006). *B. tectorum* is considered a habitat generalist (Chong et al. 2006), having proven itself successful in a broad range of habitats and ecological conditions in North America, including high elevations between 7,000 and 10,000 feet (Kao et al. 2008, Wade 2015, Bromberg et al. 2011). Cheatgrass exhibits a great deal of phenotypic plasticity, particularly for freezing tolerance and seedling emergence date (Griffith et al. 2014), and therefore is able to colonize areas with widely different microclimates and site characteristics. Broadly adapted generalist genotypes, expressing phenotypic plasticity, dominate historically invaded environments, while specialist genotypes dominate recently invaded salt desert and warm desert environments (Merrill et al. 2012). According to Driscoll (1964: 351), the adaptability of the cheatgrass enables it to compete successfully for niches not occupied by perennial species even in relatively undisturbed habitats. Cheatgrass shows considerable phenotypic plasticity, and is able to respond to differences in resource availability with different growth forms from a generalist genotype (Rice and Mack 1991, Leger et al. 2009, Meyer and Leger 2010).

Cheatgrass is cleistogamous (or self-pollinated), showing a high degree of homozyosity (Hulbert 1955, Mack 1981, McKone 1985, Ramakrishnan et al. 2006). Similar habitats across the range of cheatgrass select for a specific self-pollinating line from an array of widely-distributed genotypes (Ramakrishnan et al. 2006). Cheatgrass populations in Europe and Africa have much greater genetic diversity than North American cheatgrass populations, which have gone through a genetic bottleneck based on founder effect (Novak and Mack 1993, Valliant et al. 2007). Disturbances that create increased resource availability can result in cross-pollination in cheatgrass, resulting in a diversity of genetic types that allow it to occupy of a wide range of microclimates (Mealor et al 2013).

Rather than having a generalist genome, Kao et al. (2008) found that Rocky Mountain cheatgrass invasions are characterized by high levels of genetic and phenotypic variation, enabling cheatgrass to adapt to and specialize in local conditions. Montane populations of *B. tectorum* are comprised of a few common genetic haplotypes across the species' western North American range, genetically more similar to each other than to neighboring lowland populations (Arnesen et al. 2017). However, Arnesen et al. (2017) found evidence of lineages of cheatgrass genetically adapted to local montane conditions. Cold-grown cheatgrass has a stout basal rosette of leaves, while cheatgrass grown in warm conditions has long, flexible leaves (Griffith et al. 2014). One montane haplotype showed great phenotypic plasticity, and also was found in salt desert and sagebrush steppe habitats (Arnesen et al. 2017).

A Head-Start in Growth

Members of the *Bromus* genus can survive the winter in excellent condition (Mack and Pyke 1983, Mack 2011), and considerable growth can occur during winter months at low elevations (Hulbert 1955). While overwintering in a prostrate rosette form, it completes most of its root growth before spring (Vallentine and Stevens 1994) and then flowers and sets seeds in spring. It germinates at a wide range of temperatures (Martens et al. 1994) and as much as three days earlier than bunchgrass seeds more successfully, and at a higher rate and speed than native grasses, particularly so at low temperatures (Ray-Mukherjee et al. 2011, Hardegree et al. 2010) securing its foothold on the landscape (Warg 1938). Seed germination often follows rain or

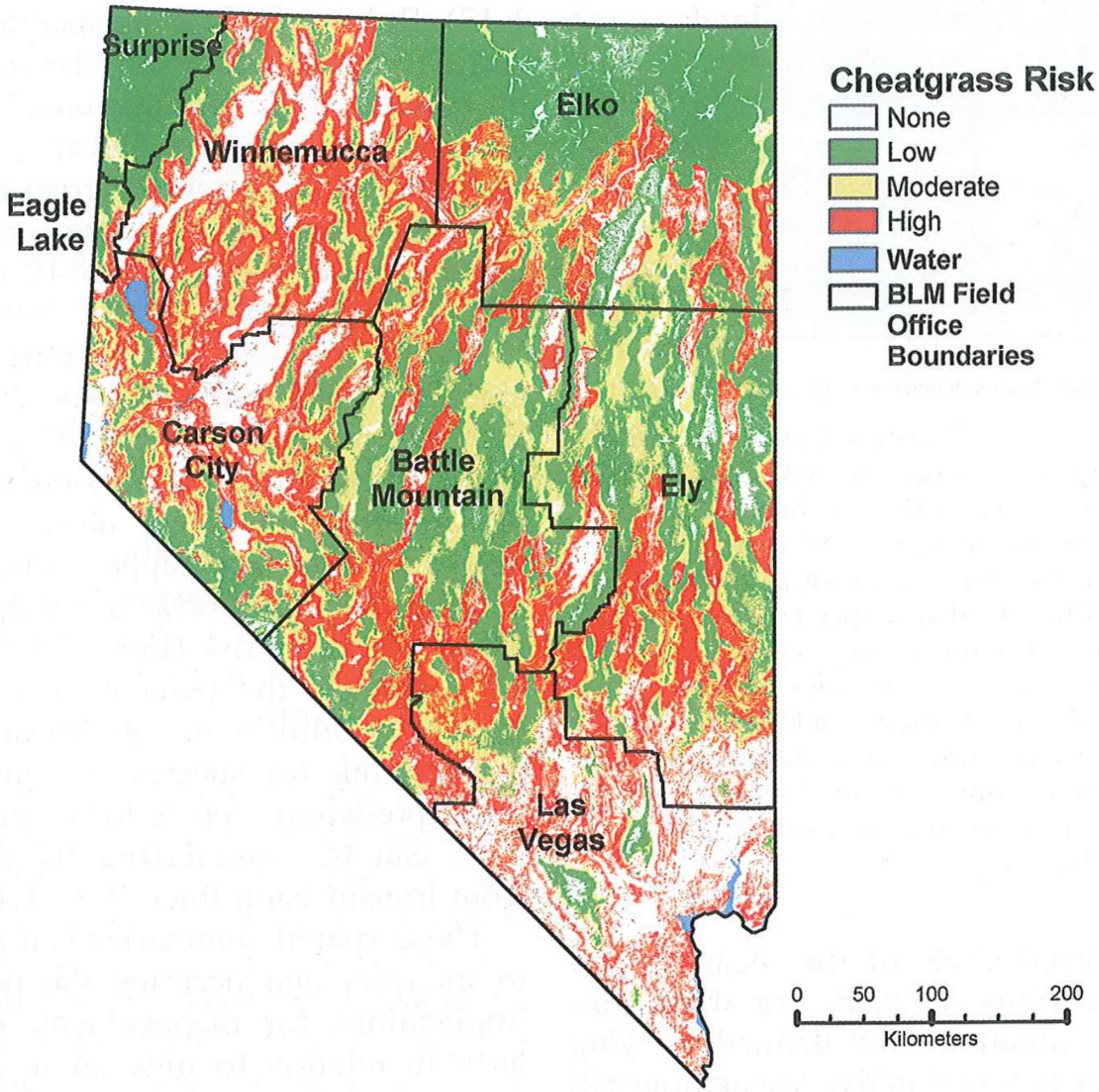


Figure 4. Risk of future cheatgrass displacement of sagebrush and other vulnerable plant communities over a 30-year time horizon. Reproduced from Wisdom et al. (2005).

snowmelt (Mack and Pyke 1984). Roundy et al. (2007) found that spring germination was more dependable than fall germination in the central and eastern Great Basin, but even during fall, cheatgrass germinates more rapidly that perennial bunchgrasses, giving it a competitive edge (Harris 1967). Most cheatgrass seeds are expected to germinate by the spring following seed set, but low autumn precipitation leads to longevity of cheatgrass seeds in the soil seedbank (Meyer et al. 2007). Cheatgrass seed germination is depressed by soil compaction, as well as by warm, dry soils or cold soils (Thill et al. 1979).

Cheatgrass shows more rapid shoot and root growth than native grasses (Arredondo et al. 1998). Cheatgrass also has a distinct advantage over bluebunch wheatgrass (*Pseudoroegneria spicata*) in its rate of root elongation at cooler temperatures (Harris 1967). Aguirre and Johnson (1991a) found that cheatgrass seedlings achieved greater root length and also greater shoot development from seed than seedlings of either crested wheatgrass or native bunchgrasses. Cheatgrass elongated adventitious roots earlier and at colder temperatures than crested wheatgrass and bluebunch wheatgrass cultivars, and bluebunch wheatgrass failed to produce adventitious roots at all at colder temperatures (Aguirre and Johnson 1991b). Cheatgrass can outcompete native grasses for water and nutrients because it is already actively growing when native plants are initiating growth (Pellant 1996, Monson 1994). By the time native perennials germinate in the spring, cheatgrass already has its root system well advanced toward full development (Hironaka 1961). Early competition from cheatgrass seedlings makes cheatgrass monocultures highly resistant to reestablishment by perennial grasses (Humphrey and Schupp 2004).

Late summer or early fall rains may be necessary to cause dense and abundant cheatgrass germination (Thill et al. 1984). Drought results in sparse germination and poor adult survival for cheatgrass (Hulbert 1955). Mack and Pyke (1983) found that 61% of seedlings sprouted in late August or September, but additional germination occurred through the winter and into the spring. But dry periods give native grasses an advantage. Native annual grasses and forbs in the Mojave Desert have small seeds that can remain dormant for long periods of time, whereas red brome seeds are larger and germinate more readily, making its populations more susceptible to being unable to outlast protracted droughts (DeFalco et al. 2003).

Perennial grasses sometimes germinate in fall but do not emerge until spring, and overwintering seedlings that do germinate are vulnerable to being killed by freezing temperatures (Boyd and Lemos 2013).

A Superior Competitor for Soil Nutrients

Cheatgrass is a fast-growing grass and shows high rates of nutrient uptake (Booth et al. 2003). Cheatgrass has a faster growth rate than native perennial bunchgrass, and thus is able to better take advantage of high nitrogen availability to fuel rapid growth and expansion (Monaco et al. 2003).

Increased nitrogen deposition at high altitudes may give cheatgrass an additional advantage over native grasses (Brown and Rowe 2004), and also increases red brome in Mojave Desert environments (Brooks 1993). High levels of soil inorganic nitrogen confer a competitive advantage on cheatgrass over native grasses, and also facilitate nitrogen loss from soils through leaching and erosion (Adair and Burke 2010). Sagebrush communities showed significantly greater nitrogen at all soil depths than either cheatgrass or crested wheatgrass communities (Austreng 2012). Rau et al. (2014) found that cheatgrass was negatively correlated with available soil nitrogen, largely because nitrogen-rich soils tend to be finer-textured and have a greater water-holding capacity. Ultimately, cheatgrass mines the soil of nitrogen, to the detriment of its competitors (Jones 2015). Cheatgrass decreases the amount of nitrogen available to soil microbes due to the low-nitrogen and high-carbon litter it produces, which in turn reduces the amount of nitrogen available to competing plants (Evans et al. 2001). Vasquez et al. (2008) found that cheatgrass competed effectively even at low levels of soil nitrogen. Thus, cheatgrass flourishes in the presence of nutrient pulses, but ultimately drains soils of available nitrogen, which helps cheatgrass exclude native grasses.

Due to its annual death and decomposition, cheatgrass invasion results in faster nitrogen cycling and availability in the soil, which promotes its own continued dominance (Stark and Norton 2015, Hooker et al 2008). Lowe et al. (2003) showed that cheatgrass gains a competitive advantage over blue grama as nitrogen availability increased; low nitrogen levels alleviated competitive pressure from cheatgrass but did not suppress cheatgrass growth. McLendon and Redente (1992) concluded that the transition from annual to perennial grasses occurred as soil nitrogen was depleted to the point where fast-growing annuals no longer had sufficient nitrogen to support high biomass production. Annuals also dominate by monopolizing spaces and light through aboveground biomass production (McLendon and Redente 1992).

Likewise, cheatgrass benefits from high levels of soil phosphorus. Rau et al. (2014) found a very strong correlation between available phosphorus in the soil and cheatgrass prevalence. McGlone (2010) found that soil nitrogen and phosphorus were greater in cheatgrass-dominated areas. Cheatgrass can liberate chemically-unavailable soil phosphorous in desert ecosystems, making it available to plants, and furthermore soils with more bio-available phosphorous have been found to be more susceptible to cheatgrass expansion (Germino et al. 2016). Thus, for both nitrogen and phosphorus, cheatgrass invasion increases nutrient availability and speeds up nutrient cycling, which provides positive feedbacks for continued cheatgrass dominance until soil nutrients become exhausted.

A Superior Competitor for Water

Cheatgrass depletes soil water in spring much more rapidly than native species, suppressing the survival of native seedlings and subjecting adult plants to moisture stress (Booth et al. 2003). Bluebunch wheatgrass seedlings growing amid dense cheatgrass suffer from moisture stress, averaging 15.8% moisture by weight, compared to 43.2% moisture for bluebunch wheatgrass seedlings growing in the absence of cheatgrass (Harris 1967). Perennial grasses have an inherent advantage over cheatgrass in undisturbed areas because they do not have to grow from seeds each year, but in disturbed areas where perennial bunchgrasses are eliminated, cheatgrass seedlings roots are able to grow faster and deeper than the roots of native bunchgrass seedlings, thereby outcompeting them for water (Harris 1977). Young and Allen (1997) and Young et al. (1987) considered that competition for water was the major factor in cheatgrass replacement of perennial bunchgrasses over time.

Unlike native perennial grasses, cheatgrass can extend its roots downward more than 80 cm during winter, allowing them to outcompete native grass seedlings (Mack 2011, and references therein). Bluebunch wheatgrass seedlings growing amid dense cheatgrass showed shallower root development, and were unable to access deeper soil moisture, unlike seedlings growing amid sparse cheatgrass (Harris 1967). Furthermore, cheatgrass develops longer lateral roots, helping seedlings to outcompete crested wheatgrass or bluebunch wheatgrass when soil water is limited (Johnson and Aguirre 1991). Cheatgrass is more efficient at extracting water from the top 0.5 m of the soil column, but mature bluebunch wheatgrass has deeper roots and can take advantage of deeper soil moisture (Pellant 1996). Native shrubs have tap roots extending 1 to 3m downward, and native grasses typically root at 10-50cm depth, while cheatgrass creates dense mats of shallow annual roots, typically within the 30-40cm depth range (Germino et al. 2016). Thus, once native plants reach maturity, they can access soil water that cheatgrass cannot exploit. Sparse, frequent rains favor *Bromus* species due to their shallow, fibrous root systems, while deep, infrequent soakings favor native grasses with deep taproots (Hunter 1991). Chambers et al. (2014: 365) observed that most plant species regardless of growth form, including cheatgrass have some shallow roots to access soil water.

A High Reproductive Rate

Cheatgrass can be a prodigious seed producer. A single cheatgrass plant can produce hundreds of seeds (Hulbert 1955, Meyer and Leger 2010), and as many as 5,000 seeds (Young et al. 1987), or as few as one seed when drought-stressed (Hulbert 1955). Cheatgrass plants that germinated in spring show markedly lower seed production (Klemmedson and Smith 1964). Billings (1994) found that the number of viable cheatgrass seeds in soil up to 15 cm deep on an unburned site was 1,177 seeds per square meter. Humphrey and Schupp (2001) found that unburned plots of cheatgrass-dominated annuals contained 99% cheatgrass seeds in their seed banks, with a density of 4,800 to 12,800 seeds per square meter. Seed production for cheatgrass ranged from 3,567 seeds per square meter during a drought year to 13,942 seeds during a high-precipitation year in western Utah (Smith et al. 2008). Meyer et al. (2007) found seed densities ranging from 8,000 to 31,000 seeds per square meter. Stewart and Hull (1949) reported cheatgrass seed densities averaging 1,646 seeds per square foot (or 17,717 seeds per square meter). Cheatgrass has copious seed production, and native grasses are not characterized by long-lived seeds; thus, cheatgrass dominates the seedbank and over time outcompetes perennial bunchgrasses even when cheatgrass begins at low densities (Young and Allen 1997, Mazzola 2008). The high density of cheatgrass seeds gives this weed a competitive advantage over native perennial grasses in colonizing bare ground (Monsen 1994).

In Idaho, cheatgrass sets seed in the third week of May (Hironaka 1961) or earlier. Cheatgrass seeds become dormant during the heat of the summer, allowing the plant to escape from moisture stress during the driest part of the year (Milby and Johnson 1987), when perennial grasses must endure drought stress. Seed germination does not appear to be a limiting factor governing cheatgrass invasion; instead, seed survival and reproductive output by adult plants are likely the most important factors (Roundy et al. 2007). Humphrey and Schupp (2001: 91) reflected on the attrition of cheatgrass seeds during the course of fire, and concluded that while fire reduced cheatgrass seed abundance for one year, *B. tectorum* never lost dominance in the seed bank.

Propagule pressure is the single extrinsic factor that seems to dictate invasion rate (Meyer et al. 2001). Undisturbed landscapes have lower propagule pressure for invasive weeds (Zouhar et al. 2008). Propagule pressure is the abundance of non-native seeds on-site and within dispersal distance (Zouhar et al. 2008). Kao et al. (2008) support the propagule pressure hypothesis – that greater numbers of seeds drive cheatgrass expansion. Kao et al. (2008: 217), highlighted the importance of preventing long-distance weed seed dispersal: "We found, however, that high- and low-elevation sites were not distinct, which suggests that resources need not be focused on movement of seed specifically within elevations, but rather movement of seeds more generally. … If propagule pressure is playing a role in the range expansion of downy brome, then preventing seed dispersal from the edge of the range could minimize its continued spread." Seed banks typically have large numbers of *Bromus* seeds in both heavily invaded and more intact community types (Chambers et al. 2016).

Humphrey and Schupp (2001) found that native perennial grass seeds were virtually absent from the seed banks of cheatgrass-invaded sites, whether they were burned or unburned. Even native colonizing species cannot keep pace with cheatgrass seed production: Squirreltail seeds germinate at much lower rates than cheatgrass (Young et al. 2003). Young and Allen (1997: 531) suggested that cheatgrass enjoys a seed production advantage over native perennial grasses as well: "Most of the native perennial grasses of sagebrush/bunchgrass communities have irregular, limited seed production, the seeds have complex dormancies and/or low viability, and most species do not build seedbanks."

Cheatgrass seeds are normally fairly short-lived, but under ideal conditions can survive for many years. Cheatgrass seeds have been kept alive for 11 years in laboratory conditions, and commonly survive 2-5 years in field conditions (Upadhyaya et al. 1986). Other researchers reported that cheatgrass seeds typically remain viable for up to four years in field conditions (Mealor et al. 2013), or at least 11.5 years (Hulbert 1955). There is broad consensus that most cheatgrass seeds germinate during their first year (Hulbert 1955, Mack and Pyke 1983, Mealor et al. 2013). Smith et al. (2008) found that cheatgrass seeds that do not germinate during the first autumn rarely remain viable beyond the second carryover year. Prevéy and Seastedt (2015) found little carryover of viable cheatgrass seeds from year to year on the shortgrass prairies of eastern Colorado. Fewer than 13% of the seeds viable in July were still present by December or March (Mack and Pyke 1983). Under normal field conditions, cheatgrass seeds persist in the seedbank for 1-3 years (Meyer et al. 2007). The abundance and persistence of cheatgrass seeds in the seed bank allows the species to persist on the landscape even following eradication treatments (Monaco et al. 2016).

Precipitation can have a major effect on seed output and survival for cheatgrass. Seedling emergence was 1,304 seedlings per square meter in a high-precipitation year, versus 270 seedlings per square meter in a drought year (Smith et al. 2008). During drought conditions, cheatgrass can shift resource allocations away from root growth and toward shoot growth and seed production, enabling them to mature more rapidly and set seed before the plant succumbs to drought stress (Rice et al. 1992).

Suppression of Competing Native Vegetation

Cheatgrass exerts a negative influence on the growth of neighboring native plants (Wade 2015). Lucero and Callaway (2018b) found that cheatgrass seedlings suppressed the seedlings of bluebunch wheatgrass and bottlebrush squirreltail by 73% and 67%, respectively, but the native grass seedlings did not suppress cheatgrass seedlings. Cheatgrass infestations suppress sagebrush seedlings as well as the growth and productivity of sagebrush in comparison with sagebrush with native bunchgrass in the understory; competition for water and to a lesser extent nitrogen during summer and fall appear to drive this relationship (Booth et al. 2003). Transpiration by densely growing *B. tectorum* depletes soil moisture in the spring, preventing establishment of native shrub and perennial grass seedlings (Harris 1967; Cline et al. 1977; Monsen 1994) and depressing the moisture status even of mature shrubs (Melgoza et al. 1990). Sagebrush seedlings in both burned and unburned cheatgrass sites experienced poor survival (Gurr and Wicklow-Howard 1992). Shrubs are important to block wind, trap soil and snow, and provide shade (Goodwin 1992). The presence of shrubs aids the re-establishment of perennial native grasses in alien-dominated communities (Goodwin 1992).

Native herbivores can also suppress native grasses by preferentially eating native vegetation and seeds. Based on exclosure experiments, Hironaka (1986) concluded that small mammal herbivory can retard the return of native bunchgrasses once cheatgrass becomes dominant. Thus, the intrinsic advantages that cheatgrass possesses in competition with native bunchgrasses are amplified by herbivory and granivory, accelerating cheatgrass' path to dominance.

Cheatgrass Changes Soil Chemistry and Structure

Invasion by non-native plants can trigger changes in soil nutrient availability and cycling (Ehrenfeld 2003). Cheatgrass invasion results in more available forms of nitrogen, which can then leach out of soils (Sperry et al. 2006). Norton et al. (2004) found that cheatgrass areas had elevated levels of inorganic nitrogen. "The loss of root biomass and increasing NO_3^- concentrations in the subsurface could result in the export of N from the system during episodic wet periods or in more mesic environments" (Rau et al. 2011: 145). Nitrogen is mineralized and leaks out of soil systems beneath cheatgrass infestations, whereas shrubsteppe soils tend to have a tight retention of immobilized soil nitrogen (Norton et al. 2004). After 10 years of cheatgrass invasion, there is essentially no nitrogen mineralization occurring in the soil, which reduces soil health and elevates cheatgrass's competitive advantage (Blank 2008). Soil ammonium levels (NH_4^+) and nitrate (NO_3^-) were higher in recently invaded sites than in noninvaded sites (Sperry et al. 2006).

Conversion of shrubsteppe to cheatgrass affects soil nutrient dynamics in much the same way as conversion of grasslands to annual row crops (Norton et al. 2004). Cheatgrass invasion either led to an increase in soil organic carbon and nitrogen availability and/or an acceleration of soil nitrogen mineralization in C_3 communities, or changes in soil biota paired with an increase in soil nitrogen cycling in C_4 communities (Schaeffer et el. 2012). Hilty et al. (2003) found that a post-burn site dominated by cheatgrass rather than reseeded by perennial grasses and contained less organic matter, than the perennial grass site. According to Norton et al. (2004), elevated soil-water content paired with lower root inputs to subsoils, and the possibility of a mineralization priming effect caused by large precipitation-induced pulses of microbial activity, may lead to the depletion of organic carbon in the subsoil beneath cheatgrass-dominated vegetation. These soil changes amplify the dominance of cheatgrass and its competitive advantages over native bunchgrasses.

Cheatgrass Alters Soil Biota

Germino et al. (2016) suggested that changes in soil biota are part of the positive feedback loop that helps cheatgrass increase its dominance once it becomes established. Cheatgrass is considered a facultative mycorrhizal species. Mycorrhizae are often commensal, colonize the root system, and can assist plant with uptake of soil nutrients. These are depleted or absent on disturbed sites for up to a decade, while cheatgrass does not require mycorrhizal symbionts, which explains in part why cheatgrass is so successful at invading disturbed lands (Wicklow-Howard 1994). Cheatgrass showed a greater propensity to be colonized by VAM in the face of competition with native grasses, less so when occurring in a monoculture (Al-Qawari 2002).

When cheatgrass grows in communities of nonmycorrhizal plants, it is nonmycorrhizal; in communities of mycorrhizal plants, it is mycorrhizal (Goodwin 1992). Cheatgrass can grow entirely independently of mycorrhizae (Wicklow-Howard 1994). Pendleton and Smith (1983) recorded no vesicular-arbuscular mycorrhizae associated with cheatgrass at one Utah site, but did record it in others.

Cheatgrass appears to benefit from vesicular-arbuscular mycorrhizae (VAM) colonization, showing greater root and shoot biomass (Al-Qawari 2002). "The success of *B. tectorum* appears closely tied to its ability to reduce and perhaps change the beneficial VAM fungal population indigenous to an area" (Al-Qawari 2002: 4). Cheatgrass is a poor host for arbuscular mycorrhizal fungi and cheatgrass can have a lasting negative effect on the VAM community

(Busby 2011). Hawkes et al. (2006) found that cheatgrass invasions decreased the richness of arbuscular mycorrhizal fungi on the roots of native grasses. Lower VAM spore counts are found in areas with cheatgrass infestations (Al-Qawari 2002). However, at a high elevation site, Rowe and Brown (2008) found that cheatgrass presence did not alter soil arbuscular mycorrhizal communities in ways that inhibited the growth of native grasses. Disturbed sites invaded by non-mycorrhizal weeds can lose their VAM assemblages for up to 10 years (Wicklow-Howard 1994). Re-establishment of mycorrhizal native plants may not occur until both soil mycorrhizae and seeds are present simultaneously (Goodwin 1992).

Goodwin (1992) hypothesized that any benefits derived from the symbiosis between mycorrhizae and native grasses would accrue equally, or perhaps even more greatly, to cheatgrass. When cheatgrass and bluebunch wheatgrass were grown together, VAM colonization was greater for cheatgrass plants than in cheatgrass monocultures, and less for the native grass than when it grew in exclusion to cheatgrass. Areas dominated by cheatgrass showed reduced VAM assemblages for an old-field site on the Southern Plains, but results from sagebrush steppe in the Piceance Basin were equivocal (Al-Qawari 2002). The ability to suppress VAM colonization in native grasses may confer a competitive advantage to cheatgrass (Al-Qawari 2002).

Following fire, mycorrhizal spores are depleted, inhibiting sagebrush re-establishment (Gurr and Wicklow-Howard 1992). Bellgard et al. (1994) found that VAM spores were less abundant in post-fire soils than in unburned soils after a moderate-intensity fire in an area with resprouting plants, but rates of plant root infection were similar on burned and unburned sites. Nonmycorrhizal plants like cheatgrass tend to be successful at colonizing disturbed sites, while the obligate mycorrhizal plants that dominate undisturbed sites have difficulty colonizing disturbed areas (Wicklow-Howard 1994, Knapp 1996). The loss of VAM mycorrhizal biodiversity could reduce plant biodiversity and productivity, and foster ecosystem instability (van der Heijden et al. 1988). Re-establishment of rangeland shrubs assists in the recovery of mycorrhizal fungi populations in the soil (Goodwin 1992), and thus sagebrush losses following fire can retard mycorrhizal fungus recovery.

Cheatgrass and Fire

The relationship between cheatgrass and fire can most accurately be described as a livestock-cheatgrass-fire cycle. Murray (1971) blamed the conversion of native bunchgrass ranges to cheatgrass on repeated burning and excessive grazing. For the western United States, Carter et al. (2014: 2) concluded that cheatgrass invasion is the result of livestock grazing altering fire frequency and resulting in a vegetative type transition.

Brooks et al. (2015) link livestock grazing to reduced fire frequency and juniper expansion in high-elevation habitats, but fail to clearly elucidate the clear link between livestock and cheatgrass, and therefore the more frequent fires that are the primary subject of the report. Carpenter and Murray (2005: 5) described the livestock-cheatgrass-fire cycle as beginning with disturbance (typically heavy grazing) followed by and invasion of cheatgrass and other annuals resulting in increased fire frequency that spreads to other vegetation types, feeding back into site deterioration in the form of erosion and nutrient loss. Seefeldt and McCoy (2003) found on the U.S. Sheep Experimental Station that following fire, spring- and summer-grazed pastures converted to high cheatgrass cover while the fall grazing and rest pastures recovered with little cheatgrass cover.

Fire favors invasion of non-native plants where nonnative seeds are abundant and/or the native species are stressed (Zouhar et al. 2008). Grass invasions in shrublands create fuel continuity, increasing fire frequency, size, and completeness of burning (Brooks 2008a). Cheatgrass-invaded areas showed significantly greater fire frequency, size, and occurrence compared to uninvaded sites (Fusco et al. 2019). Fire spread was extensive and rapid where *Bromus spp.* were prevalent (Brooks 1999b). Fire can negatively affect biological soil crusts, with decreases in abundance and diversity, and effects lasting at least two decades (Root et al. 2017). Fire can provide surges of key resources, including light, water, and/or soil nutrients, increasing the potential for invasive species to establish (Zouhar et al. 2008). When fire regimes change with

As this photo from Oregon's Hunting Valley shows, heavy disturbance or overgrazing leads to cheatgrass dominance in the understory (at right), increasing fine fuels and flammability. When invaded shrublands burn (at left), sagebrush and other fire-intolerant plants are eliminated, resulting in cheatgrass monoculture. Matt Lavin photo courtesy Flickr Creative Commons.

cheatgrass dominance, the increased costs of fire prevention and suppression that result may exceed a billion dollars nationwide each year (Pyke et al. 2016).

Large patches of shrubsteppe were historically resistant to fires due to possessing a perennial bunchgrass understory (Knick and Rotenberry 1997). Cheatgrass accelerates fire return interval substantially, and is promoted by heavy livestock grazing (Mclver et al. 2010). Bukowski and Baker (2013) used General Land Office Survey data to determine fire rotations of 171-342 years in Wyoming big sagebrush and 137-217 years in mountain big sagebrush habitats. Brooks et al. (2015) reported modern fire rotations in the western region of the greater sage-grouse range ranging from 61 to 150 years in big sagebrush and 97 to 458 years in low/black sagebrush. The eastern region showed much longer fire rotations for sagebrush habitats, ranging from 445 to 7,533 years. The shortening of these rotations in the western region demonstrate the influence of cheatgrass invasion. According to Vasquez et al. (2008: 288), the plant community is easily transitioned to an annual-grass-driven system when fire frequency increases. In the Mojave Desert, native plants do not produce sufficient fine fuels or accumulated litter in interspaces between shrubs to carry a fire, whereas cheatgrass and red brome now create continuity of fuels sufficient to carry fires across interspaces in invaded areas (Brooks 1999b). Fire was once rare in hot deserts like the Mojave and Sonoran, but due to weed invasion, fire is now becoming more frequent (Brooks and Chambers 2011).

Increased prevalence of fire in sagebrush ecosystems is strongly associated with cheatgrass invasion (Brooks et al. 2015). Cheatgrass can create positive feedbacks with fire to expand its own range and dominance (Brooks and Chambers 2011, Boyte and Wylie 2016). Bradley et al. (2017) found that lands with at least 15% cheatgrass cover were twice as likely to burn as lands with lower abundance, and four times as likely to burn multiple times over a 15-year span than lands with low cheatgrass abundance. D'Antonio and Vitousek (1992: 73) postulated that this feedback loop may be because invasive annuals recover faster than native species. Brooks et al. (2004) proposed an invasive plant/fire model in which invasive plants are introduced, then become "naturalized" (self-sustaining), then become invasive by spreading beyond the original introduction site, then change the fire regime by altering fuel loads, fuel properties, and horizontal continuity of fuels. This often leads to a positive feedback loop that further solidifies the invasive species' dominance. The damage cheatgrass causes as a competitor to native plants is eclipsed by the role that it plays after death in forming highly combustible tinder in summer, to fuel wildfires (Mack 2011).

In the western Great Plains, fire does not appear to facilitate the expansion of cheatgrass, with burned areas showing reduced densities of cheatgrass (Porensky and Blumenthal 2016). Vermeire et al. (2018) asserted that cheatgrass is ephemeral on the Great Plains, in contrast to its tendency for persistence in the Great Basin. In some cases, fire actually reduces cheatgrass on the Great Plains (Stohlgren et al. 2009, Vermeire et al. 2018). Japanese brome and soft chess may be reduced by fire because they depend for seedling establishment on soil moisture retained by litter layers (Zouhar et al. 2008). Ripgut brome decreases after fire because its seeds are not protected from the heat (DiTomaso et al. 2006). Vermeire et al. (2018) suggested that on the Great Plains, livestock grazing, fire, and cheatgrass are largely independent of one another.

The amount of fuel, called fuel load, is a primary determinant of fire intensity (Brooks et al. 2004). Davis and Nafus (2013) found that cheatgrass-invaded grass communities were characterized by higher fine fuel loads, greater fuel continuity, and lower fuel moisture content than non-invaded communities. Standing dead stems often serve to spread fire through otherwise sparsely distributed perennial vegetation (Stewart & Hull 1949; Mayeux et al. 1994). At their eastern Oregon study site, Davies and Nafus (2013) found that fuels cover more than 90% of the ground in invaded communities, versus 60% in uninvaded communities.

The more frequent and larger fires that are correlated with cheatgrass invasions do not necessarily translate into hotter fires. McIver et al. (2010) argued that because cheatgrass is highly flammable, it increases the likelihood of hot fire. However, fires in cheatgrass tend to be of relatively low temperature, and even repeated fires do not have a long-term effect on soil carbon or nitrogen (Jones et al. 2015). Temperatures lethal to cheatgrass seeds are seldom reached in range fires (Klemmedson and Smith 1964). The cooler temperatures in cheatgrass monoculture fires can preclude native grass recovery because cheatgrass seeds survive the fire in great numbers to recolonize the burned area (Kulpa et al. 2012, Germino et al. 2016). Thus, cooler fire temperatures in cheatgrass monocultures facilitate a more rapid transition back to cheatgrass (Brooks 2008a). Cheatgrass litter may insulate the soil from the heat of fires (Jones et al. 2015), allowing cheatgrass seeds to survive.

The highly mechanized nature of modern society contributes to an elevated fire frequency that favors cheatgrass, through human-caused ignition sources (Reid et al. 2008). The close association between humans and cheatgrass, with infestations concentrated along roads and railroads, and the close association between human activity and fire ignitions, further add to the synergy between cheatgrass infestations and fire (Bradley et al. 2018). Fire in cheatgrass-invaded areas was particularly associated with human activity, with 74.5% of the fires in cheatgrass-invaded areas initiated by a human-caused ignition; fireworks were a particularly major ignition source in cheatgrass-dominated environments (Bradley et al. 2017). Bradley et al. (1988) found that some 88% of fireworks-related fires occur in cheatgrass versus other vegetation types. Increase in human habitation and activity on rangelands also result in more ignitions, with 43% of the fires on the Jarbidge BLM Field Office during the two decades since 1987 being human-caused (Launchbaugh et al. 2008).

Cheatgrass invasion increases fire frequency by increasing the fuel surface-to-volume ratio, increasing horizontal fuel continuity, and creating a fuel packing ratio that facilitates ignition (Brooks et al. 2004). Fire risk, defined as the likelihood of establishing a fire with a single ignition attempt, ranged from 46% with 12% cheatgrass cover to 100% with cheatgrass cover reached 45% or more (Link et al. 2006). Bradley et al. (2017), by contrast, found that fire frequency increased substantially once cheatgrass cover exceeded 1%, but did not differ significantly between the higher cheatgrass cover values. Fires are more likely to start in cheatgrass than in native vegetation types, and cheatgrass fires were larger and burned longer than in other habitat types (Balch et al. 2013). Johnson et al. (2006) caution that while many studies of cheatgrass response to fire are performed using prescribed fire, actual range fires occur during hot dry periods of extended drought and high wind, conditions under which prescribed fires rarely are set.

Small components of cheatgrass, however, may not increase fire risk. Bradley et al. (2017) found that areas where cheatgrass occupied less than 1% cover were no more likely to burn than on lands where cheatgrass was absent. However, once cheatgrass cover reaches 1-5%, fire risk increases (Bradley et al. 2018).

Cheatgrass invasion creates larger and more frequent fires by creating continuity of fine fuels (Whisenant 1990, Brooks et al. 2004, Condon and Pyke 2018, Young et al. 1987). Knick and Rotenberry (1997) observed that high connectivity of annual grasslands increases fire spread even when fire frequency is low. Pilliod et al. (2017) found that native perennial grass production plus cheatgrass litter helped to predict fire size, while frequency of fire ignitions was not associated to plant production. Whisenant (1990) observed that cheatgrass invasion leads to larger fires, with fewer patches of unburned vegetation within the fire perimeter.

Large rangeland fires in the Intermountain West largely occur in areas with an abundance of exotic grasses (Knapp 1998). However, native grasses can also sustain very large fires during extreme weather (typified by drought, high wind, and high temperatures). Pilliod et al. (2017) found that weather was the greatest single factor in predicting fires; the A dry year (with a dry spring) following a wet year (supporting fuel accumulation) was the best predictor of fire frequency and size (Pilliod et al. 2017).

The Murphy Fire Complex burned more than 600,000 acres in Idaho and Nevada in 2007 in predominantly native bunchgrasses and plantings of non-native bunchgrasses such as crested and intermediate wheatgrass (Launchbaugh et al. 2008). Large fires are most frequent in summers following a year of near-normal or wetter precipitation, which maximizes grass growth and fuel loading (Knapp 1998). Whisenant (1990) found that while fine fuels increased as cheatgrass frequency increased, this relationship that did not hold for native bunchgrasses. The reason, according to Whisenant (1990), was that more pristine areas contained native grasses, which did not increase fine-fuel frequency. But cheatgrass invasions may result in less-intense fires, as woody fuels are burned away (Brooks et al. 2004).

Cheatgrass invasion definitively increases fire frequency. The establishment of cheatgrass creates a cycle of accelerating range fire frequency, with fire return intervals as short as 3 to 5 years (Pellant 1996, Whisenant 1990). Balch et al. (2013) found that 13% of cheatgrass-dominated areas in the central Great Basin had burned between 2000 and 2009, generating a 78-year fire return interval (more than double non-cheatgrass sites, which were much less prone to large fires as well). Across multiple datasets, subsequent research found that cheatgrass fire return interval ranged from 50 to 78 years; by contrast, sagebrush habitats showed a fire return interval of 196 years (Balch et al. 2013). Whisenant (1990) pointed out that it is the continuity, rather than the amount, of fine fuels dictate the frequency of large fires.

Cheatgrass extends the fire season into months when native sagebrush steppe would rarely burn under natural conditions (Davies and Nafus 2013). Cheatgrass dries rapidly in late May and June, providing abundant fuel for extensive range fires through the month of October (Billings 1994). An earlier onset of fire season and a lengthening of the window during which conditions are conducive to fire ignition and growth further the fire-invasive feedback loop (Brooks et al. 2004, Abatzoglou and Kolden 2011). According to Blank et al (2006: 234), "In the intermountain west of the USA, where *B. tectorum* is so dominant, by late spring to early summer the fuel is extremely flammable, ready to burst into a wildfire given the chance of ignition." Brooks et al. (2015) found that fire season is lengthening in some areas (e.g., the Southern Great Basin), but other areas are showing a shorter fire season (notably the Great Plains).

Cheatgrass accelerates fire frequency because fine fuels are much more abundant in cheatgrass-invaded areas than in undisturbed native sagebrush and shadscale vegetation types (Knapp 1996). Increase in fuel continuity means that cheatgrass-invaded grasslands burn more continuously, with less of the patchy mosaic that is found with burns in uninvaded grasslands (Davies and Nafus 2013). As a result of changes in fine fuels, cheatgrass communities were 3.5 to 4 times more likely to burn in the 1980s and 1990s than native plant communities (Balch et al. 2013).

Fires create a nitrogen-rich soil environment, particularly beneath burned shrubs, ideal for cheatgrass colonization (Young and Evans 1978). Over the longer term, fire can result in small losses in ecosystem nitrogen (Hooker et al. 2008). However, Chambers et al. (2007) found that burning had no effect on soil nitrate. Disturbances and fire lead to increased soil mineralization, and this accelerates cheatgrass invasion (Young and Allen 1997). Hobbs and Huenneke (1992: 327) observed, "In some cases, fire per se does not affect the degree of invasion, or will only do so when combined with some other type of disturbance, such as mechanical disturbance of the soil or nutrient input." Fire disturbance eliminated shrubs and suppressed soil crusts, leaving a void for cheatgrass to increase (Condon and Pyke 2018). Smith et al. (2023a) found that the majority of areas that transitioned to cheatgrass dominance since the 1990s did so in the absence of fire within the previous decade, and conclude that fire needs cheatgrass more than cheatgrass needs fire.

Cheatgrass abundance and occurrence was strongly associated with recent burns (Williamson et al. 2019). When fires burn through cheatgrass-infested areas, exposed soils create an ideal environment – a vacant ecological niche – for cheatgrass seed germination (Knapp 1996, Pilliod et al. 2017). Cheatgrass expansion following fire can be particularly severe on south-facing slopes (Kulpa et al. 2012). Porensky and Blumenthal (2016) found that cheatgrass had a slight affinity for southeast-facing slopes in the western Great Plains.

Once cheatgrass becomes widespread and abundant in the wake of fire, it remains an abundant component of the vegetation thereafter (West and Yorks 2002). West et al. (1984) found that cheatgrass persisted 13 years after fire in west-central Utah, and bunchgrasses failed to recover. By contrast, West and Hassan (1985) found that for rangelands in relatively good condition, cheatgrass increased from a minor component to dominance immediately following fire, but native bunchgrasses also recovered, reaching their pre-fire levels of cover by year two.

Woodland fires can also accelerate cheatgrass invasion. Fires in late-succession pinyon-juniper woodland were most likely to result in cheatgrass invasions, whereas in mid-successional woodlands, fire in areas with a mix of cheatgrass and native grasses resulted in a similar mix post-fire (Bates et al. 2013). However, late-successional juniper woodlands are difficult to burn due to a lack of understory fuels (Bates et al. 2011). In pinyon-juniper woodland, cheatgrass production was sufficiently high to carry a fire when soil nitrogen levels were above 3.2 grams per meter (Rao and Allen 2010).

In Rocky Mountain National Park, areas that burned had 4 to 5 times larger cheatgrass patch area and a higher percentage cover than unburned areas (Banks and Baker 2011). Billings (1998) reported that cheatgrass was the most abundant plant after a range fire in 1948, and after 40 years had increased its density on the burned site by an order of magnitude. At sites across the Great Basin, Roundy et al. (2018) found that burning increased cheatgrass cover at some sites, while increasing perennial forb cover at others.

In the absence of livestock grazing, cheatgrass colonization of burn areas may not always be widespread. Taylor et al. (2014) observed, "Our results, in the northeast region of the biome, suggest that *B. tectorum's* response to fire can be very ephemeral, and much less pronounced than the response of native perennial bunch and rhizomatous grasses."

Cheatgrass is fire-tolerant, surviving fires as seeds on or below the soil surface (Pyke et al. 2016). Wildfires generally occur after cheatgrass has dropped its seeds, but the seeds of perennial grasses are still attached to the plant (Warg 1938). Cheatgrass seeds can be depleted by fire, and this causes a one-year delay in cheatgrass expansion within burned areas (Miller et al. 2013). Humphrey

In areas where native bunchgrasses dominate the understory, fires result in native grasslands, like this expanse of bluebunch wheatgrass near Jarbidge, Nevada, rather than cheatgrass dominance. Matt Lavin photo courtesy of Flickr Creative Commons.

and Schupp (2001) found that following fire, cheatgrass seeds were less than 3% as dense as on unburned plots but recovered to pre-fire levels within two years. In the immediate wake of fire, cheatgrass makes up for low densities with increased seed production. Young and Evans (1978) found that cheatgrass plants in burns produced more than three times the seeds of plants outside burns. Cottam and Evans (1945) attributed abundance of cheatgrass in Utah's Red Butte Canyon to frequent fires near its mouth. Davies et al. (2012b) showed rapid cheatgrass colonization following fire in some areas, reduction following fire in others.

Cheatgrass densities increase dramatically 3 to 4 years post-fire (Kulpa et al. 2012). Piemeisel (1938) found that it took three years post-fire for cheatgrass to take over old fields. Density of cheatgrass plants in the year following burning was less than 10 plants per square meter, but by three years after burning, density was more than 10,000 plants per square meter (Young and Evans 1978). By year three after fire, cheatgrass had closed the community to seedlings of perennial grasses, irrevocably altering succession to a sagebrush/perennial grass equilibrium (Young and Evans 1978). Similarly, in disturbed sagebrush habitats in northwest Colorado, cheatgrass began to dominate in the third year, and perennial grasses began to appear in the fourth year (McLendon and Redente 1992). Piemeisel (1951) characterized cheatgrass as dominating succession following disturbance from year five onward.

In Colorado, Shinneman and Baker (2009) found that burns were initially dominated by native forbs, followed by native grasses by year 3, with cheatgrass expanding rapidly to dominance after 4 to 7 years, and cheatgrass ultimately declined after 9 years post-fire. Regarding cheatgrass, Hosten and West (1994: 60) found that cheatgrass cover increased dramatically following wildfire and cattle disturbance, with maximum cheatgrass cover occurring during the second-year post-fire. Bollinger and Perryman (2008) found that cheatgrass increased steadily on certain soil types twenty years post-fire, while other soil types showed fluctuating cheatgrass abundance, heavily influenced by precipitation. Cheatgrass may remain dominant 15 years post-burn (Reed-Dustin et al. 2016). Reid et al. (2008) suggested that frequent cheatgrass-fueled fires, at an interval of 3 to 6 years, could deplete perennial grasses. Fires linked to cheatgrass also facilitate the spread of other weeds such as Russian thistle and halogeton (Knapp 1996).

Cheatgrass invasion has the greatest impact on fire frequency in low- to mid-elevation habitats where it increases fine fuel continuity and pushes species with low fire tolerances out of the vegetative community (Brooks and Chambers 2011). According to Davies et al. (2012b), this is especially true at low elevation sites because the *B. tectorum* fuel structure promotes extensive and severe fires. As a result of fires on the Dugway Proving Ground in Utah started by military ordnance explosions, invasive annuals dominate many sites even though livestock had been absent for almost 50 years (West 1994).

Some researchers (e.g., Ricca and Coates 2020) point to the cheatgrass-fire cycle as a major cause of disturbance in the sagebrush biome, without mentioning the pivotal role that livestock grazing plays as a primary impact on the resilience of native sagebrush ecosystems, the loss or degradation of which is a prerequisite to cheatgrass invasion. As discussed subsequently under the 'State and Transition' section of this article, livestock grazing is the ecological switch that degrades native vegetation and facilitates cheatgrass invasion, initiating and then perpetuating the cheatgrass-fire portion of the cycle.

Cheatgrass-Invaded Communities' Response to Fire

Fire reduces near-term site resistance to cheatgrass invasion, particularly on rangelands actively grazed by livestock (Condon and Pyke 2018). This occurs as a result of multiple factors. Fires can amplify cheatgrass invasion due to short-term pulses of soil nutrients, and longer-term nutrient inputs from the decomposition of the root systems of shrubs killed by the fire (Chambers et al. 2007). Destruction of biological soil crust due to fire reduces nitrogen fixation and water infiltration rates and increases soil erosion (Johansen 1981). Chambers et al. (2007) found that while fire removes shrubs, this has a marginal effect on soil moisture availability. Post-fire, invasion by cheatgrass is limited on areas where perennial grasses and forbs resprout in abundance (Anderson and Inouye 2001).

The most abundant shrub of the Intermountain West, *Artemisia tridentata* (big sagebrush), does not resprout following fire (Blaisdell 1953, Hosten and West 1994, Knapp 1996, West and Young 2000), thus its displacement by *Bromus spp.* can persist for decades (Pellant 1990; Whisenant 1990; Knapp 1996). Neither do other sagebrush species, with the exception of silver sagebrush and three-tip sagebrush; these latter species can resprout from stumps after they burn (Brooks et al. 2015). Sagebrush seeds can survive in the seedbank through a fire, and contribute to post-fire recovery of this shrub (Condon et al. 2011). Sagebrush recovery post-fire is positively correlated with native bunchgrass cover, and declines with increasing cheatgrass density (Condon et al. 2011, Shriver et al. 2019).

Likewise, shadscale (*Atriplex confertifolia*) does not resprout from rootstocks following fire (Knapp 1996). Cheatgrass-driven fires have also caused major reductions in antelope bitterbrush communities in Idaho, Utah, Oregon, and southern California, to the point where these plant communities have become rare (Monsen 1994). Fire therefore results in the long-term elimination of most sagebrush species, and some other shrubs as well. Sagebrush populations continue to decline for years following a fire, particularly on drier, lower-elevation sites, and fires sometimes lead to local sagebrush extirpations (Shriver et al. 2019).

Cheatgrass increases with frequent burning, even in areas protected from grazing (Pickford 1932). Perennial grasses can be killed by repeated burning from short-interval cheatgrass fires (Stewart and Hull 1949). Dustin et al. (2016) found that both cheatgrass and Sandberg's bluegrass increased after fire in the absence of livestock grazing in both juniper woodlands and sage steppe communities, while bluebunch

Sagesteppe with heavy cheatgrass infestations in the understory, like this area northwest of Boise, Idaho, are particularly vulnerable to fire after the cheatgrass dies for the year and dries out. Matt Lavin photo courtesy Flickr Creative Commons.

wheatgrass decreased. On the other hand, Taylor et al. (2014) found that in the absence of livestock grazing, native bunchgrass cover increased significantly 11-15 years post-fire. Burning resulted in higher emergence but lower survival for cheatgrass (Chambers et al. 2007). After fire, competition from cheatgrass reduces the root systems of native species (Melgoza and Nowak 1991). Cheatgrass abundance, as well as native grasses, increased over time after fire; cheatgrass increases dramatically in certain years, surpassing the increase in native grasses (Shinneman and Baker 2009). Fire interiors that remained unseeded did not have higher cover of cheatgrass than unburned woodlands, but burn edges did show a higher cover of cheatgrass (Getz and Baker 2008). This result suggests a positive effect of seed production at the edges of burns disproportionately increasing cheatgrass densities along burn perimeters. Limited seed dispersal distances, in the absence of seed dispersal via livestock, could also play a role.

Condon and Pyke (2018) found that neither fire nor grazing produced direct effects on cheatgrass cover, but instead the impacts of fire and livestock were expressed indirectly through alteration of other biotic factors. The strongest predictor of postfire cheatgrass cover is pre-fire cheatgrass cover; post-fire cheatgrass cover was determined positively by cheatgrass seedbank, growing season precipitation, soil nitrogen, and negatively by tree canopy coverage and increasing fire intensity, with sunlight hours in fall and summer also playing a role (Keeley and McGinness 2007). Lichen biocrusts, a buffer against cheatgrass invasion, decreased on grazed sites as a result of fire, and did not increase in the years following fire (Condon and Pyke 2018).

This portion of the Idaho National Laboratory, ungrazed by livestock, burned in 2004. Where sagebrush understories are comprised of healthy native bunchgrasses, cheatgrass infestations do not occur, even following fire. Matt Lavin photo courtesy Flickr Creative Commons.

Brooks et al. (2004) reported that altered fire regimes stemming from cheatgrass invasion result in multiple negative effects on natural resources, local economies, and public safety, including loss of wildlife habitat, subsequent invasions by other alien species, altered watershed function, loss of tourism, and increased fire-associated hazards. These researchers recommended that species with a high potential to cause altered fire regimes must be prioritized for control, and that restoration of the preinvasion plant community, fuel, fire regime, and other ecosystem properties are necessities.

Response of Intact Plant Communities to Fire

Conversely, sagebrush steppe is typically more resilient to cheatgrass after fire in the absence of grazing and other disturbance (Seefeldt et al. 2007, Ponzetti et al. 2007). According to Anderson and Inouye (2001: 553), "the bulk of the evidence available suggests that where native plant populations in sagebrush steppe are thriving, *B. tectorum* does not pose the threat that it does where populations of native perennials have been depleted." Areas with abundant native bunchgrass that are subjected to fire return to bunchgrass, rather than cheatgrass (Hoover and Germino 2012). Fires in Wyoming with abundant perennial grasses experienced no significant increase in annual grasses post-fire, but did show increases in perennial grass productivity (Cook et al. 1994). Sites with higher bunchgrass cover may actually show greater site resistance to cheatgrass invasion following fire (Condon and Pyke 2018). In an area rested from livestock grazing, Bowker et al. (2004) found little increase in cheatgrass following fire. In a literature review limited to natural fires in areas dominated by native plants, no studies found that cheatgrass eventually comes to dominate these sites (Johnson et al. 2006).

Perennial grasses vary by species in their resilience to fire, but generally are able to survive all but the hottest fires (Wright and Klemmedson 1965). Perennial grasses tend to re-sprout following fire (Zouhar et al. 2008). Comment more about shrubs and sage than cheatgrass. Chambers et al. (2007) found that soil water and nitrate availability increased with the removal of herbaceous perennials but burning without removal provided only minor effects. Biological soil crust and bunchgrass recover well in ungrazed areas after they burned (Ponzetti et al. 2007). The recovery of bunchgrasses following fire is not immediate. Ellsworth et al. (2016) found bunchgrasses on burned plots decreased in cover during the first year post-fire but showed more than a threefold increase in cover versus unburned control plots 17 years post-fire. Postfire recovery of native plants is greater when shrubs were present prior to the burn (Kulpa et al. 2012).

In intact perennial bunchgrass communities, fire does not result in an increase in cheatgrass, and indeed native perennial grasses tend to increase post-fire (Chambers et al. 2007). In fact, perennial grasses may even expand following fire in the absence of cheatgrass (West and Yorks 2002). According to Chambers et al (2017: 117), "Soil water and nitrate availability increase following either fire or removal, but on intact sites native perennials typically increase following fire, limiting *B. tectorum* growth and reproduction." Garner et al. (2019: 100) found that management intervention may not be necessary following disturbances such as wildfire in areas with high resilience and resistance to cheatgrass invasion as a result of the prevalence of native perennial grasses and forbs. On Hart Mountain National Wildlife Refuge (where livestock have been excluded since 1992), Wroblesky and Kauffman (2003) found that prescribed fires ignited 6 years after cessation of grazing did not stimulate an increase in cheatgrass, which remained at 2% cover both before and after the fires.

Shrub presence can have a significant effect on the intensity of fires. The Murphy Complex fires, which burned on lands dominated by native grasses, grassland habitats of all types predominantly burned with low severity, whereas shrubsteppe habitats burned with about equal likelihood of low or moderate severity (Launchbaugh et al 2008). Sagebrush recovery from fire is slow, taking decades (Shinneman and McIlroy 2016). Natural recruitment of Wyoming big sagebrush occurs over time following fire assuming that a seed source is present in the area, regardless of whether the area is seeded or not (Eiswerth et al. 2009). Higher elevation sites have higher soil moisture, allowing sagebrush seedlings to grow more quickly out of high-mortality small size classes following fire (Shriver et al. 2019). Ninety percent of sagebrush seeds fall within 2m of the plant, and sagebrush seeds remain viable for approximately one year (Eiswerth et al. 2009). On Hart Mountain National Wildlife Refuge, after 30 years of protection from livestock, sagebrush cover returned to 59% of pre-fire levels seventeen years post-fire (Ellsworth et al. 2016). Reis et al. (2019) found that native grasses dominated burned areas 17 years post-fire on Hart Mountain National Wildlife Refuge. Furthermore, there were no significant differences in cheatgrass cover between burned and unburned plots on the ungrazed Hart Mountain study area (Ellsworth et al. 2016), indicating that fire may have no effect on cheatgrass density in the absence of livestock. Lavin et al. (2013) found that while shrub diversity is affected by fire in ungrazed sagebrush steppe, herbaceous plant diversity was unaffected.

Ultimately, livestock grazing drives the cheatgrass-fire cycle. According to McIver (2010), at low- to no-grazing, native grasses and forbs remain dominant post-fire, and fire returns the system to the reference state. At moderate levels of livestock grazing, habitats experience a decline in native perennial grasses. With heavy livestock grazing, perennials are replaced by cheatgrass, and fire creates a negative feedback loop, returning the areas to cheatgrass monoculture. According to Johnson et al. (2006: 64), "The conclusion to be drawn from the available data is that nonnative plant species [i.e., cheatgrass] do not typically persist at high levels or dominate in predominantly natural areas in any of the reviewed systems after wildfire."

How Cheatgrass Seeds Spread

Animals play a key role in dispersal of *Bromus spp.* seeds over distances greater than a few meters (Chambers et al. 2016). Long-distance seed dispersal for invasive weeds typically is associated with human activities, while seed dispersal by animals through endozoochory (ingestion and defecation) or epizoochory (seeds hitching rides in fur or hides) promotes "naturalization," or the spread of invasive plants beyond the initial site of colonization (Schiffman 1997, Vavra et al. 2007: 66). Cheatgrass can be spread by awns attached to the fur on animals, and cheatgrass seeds may also remain viable after passing through the digestive systems of cattle (Mealor et al. 2013).

Hurlbert (1955) found that cheatgrass seeds can disperse up to one meter in the wind. On bare ground, Johnston (2011) found that cheatgrass seed dispersal distance averaged 2.4 m, only 5% of seeds traveled farther than 7.6 m, and the maximum recorded distance was 20.8 m. After fire, vegetation cover is radically reduced, and ground windspeeds are higher, and as a result cheatgrass seed dispersal distance due to wind is farther, up to 22 m (Monty et al. 2013). Nonetheless, in the absence of livestock and human activity or fire, the ability of cheatgrass to move is limited to a few meters' distance.

Invasive plants tend to be ecological generalists that can be dispersed via a variety of animals, rather than single animal specialists (Schiffman 1997). Areas with livestock grazing often support a large number of non-native plants, which contributes to propagule pressure (Zouhar et al. 2008). Cattle increase weed abundance by dispersing seeds and increasing propagule pressure (Schiffman 1997). There is a potential for livestock to become vectors of weed seed dispersal while stressing desirable native grasses post-fire (Zouhar et al. 2008), which lends support for the common practice of resting lands that have burned from livestock grazing for several years post-fire.

Endozoochory

Janzen (1994) hypothesized that weedy grasses evolved seeds with hard coats to survive passage through the digestive tract of large herbivores and thus allow animal dispersal of the seeds to suitable habitats. Pyke (2000) observed that while many studies had postulated animal transport as a primary means of cheatgrass seed dispersal, no studies had attempted to quantify this. From field-collected fecal samples in two research rangeland areas of the interior northwestern United States and subsequent studies of seed germination in greenhouses, Bartuszevige and Endress (2008) estimated that domestic cattle disperse 1,200,000 germinable exotic seeds per square kilometer — about two orders of magnitude greater than that estimated for the native ungulates in the same area (elk [*Cervus elaphus*] and mule deer [*Odocoileus hemionus*]). Unsurprisingly, cheatgrass seeds can pass through the simple guts of wild horses, and King et al. (2019) found that cheatgrass seeds germinated from 8 percent of fecal samples from wild horses. Loydi and Zalba (2009) found that seed sprouting of a related *Bromus* species in the dung of free-roaming equids on the Argentine pampas was quite rare (a single instance), and overshadowed by native seed sproutings in the same dung. Over 70% of viable seeds in cattle feces were found to be exotic grass species, versus 34% of viable seeds in elk feces (Bartuszevige and Endress 2008). Cattle are predicted to spread 1.78 million seeds/km^2 in the Wallowa Whitman National Forest of northeastern Oregon every year, 70% of which are non-native grasses (Bartuszevige and Endress 2008).

Blackshaw and Rode (1991) and Chambers et al. (2016) asserted that *Bromus* seeds lack the attributes necessary to survive a trip through the ruminant digestive system to successfully sprout following defecation. Chuong et al. (2015) found that *Bromus hordeaceus* was carried by cattle in their pelage, but viable seeds were not passed through their digestive system. Vallentine and Stevens (1994) contended that cheatgrass seeds are readily distributed mechanically by grazing animals by having barbed spikelets that attach to the pelage, but also by incomplete digestion. *Bromus hordeaceus* seeds have been found to sprout from the dung of cattle (Malo and Suarez 1995).

Epizoochory

Invasive annual grasses produce seeds with morphologies consistent with epizoochory (Schiffman 1997). Cheatgrass seeds have barbed lemmas and sharp calluses that facilitate their dispersal to new locations by being picked up and carried in clothing or animal fur (Hulbert 1955, Chambers et al. 2016). Cheatgrass seeds may have single or multiple awns, in the latter case made up of sterile florets, and these multiple-awn seeds are more readily carried greater distances in animal fur (Monty et al. 2017). Cheatgrass seeds that are lodged in the fur, hides and especially wool of

Cheatgrass infestation along a highway in central Nevada. Note that in this case the invasion has not not spread into surrounding habitats. Matt Lavin photo courtesy of Flickr Creative Commons.

animals are readily spread (Mack 1981, Vallentine and Stevens 1994, Wessels et al. 2008), and the awned seeds of cheatgrass could have been carried for long distances by nomadic herds of sheep (Young and Allen 1997). Cheatgrass seeds commonly lodge in human clothing, and readily survive the laundry (Lefcort and Lefcort 2014). Animals with straight hair may be less prone to transporting cheatgrass seeds than those with curly pelage; Heinken and Raidnitschka (2002) documented seeds of *Bromus tectorum* carried in the pelts of European wild boar, but not roe deer. According to Getz and Baker (2008), cattle can spread cheatgrass seeds lodged in their hide, and can also prepare a favorable disturbed seed bed when they trample or graze an area. In Europe, Wessels et al. (2008) found cheatgrass seeds commonly transported in the pelage of domestic sheep. Cheatgrass seeds can also be carried in dried mud attached to the hooves or fur of ungulates. Larger herbivores likely transport mud and intact seeds over longer distances (Olff and Ritchie 1998).

Knapp (1996, references omitted) summarized the domestic livestock – cheatgrass relationship as follows: “It is likely that the domination of cheatgrass would not be as great today without the introduction of livestock. Livestock facilitate the spread of cheatgrass by two means. First, excessive grazing reduces the native herbaceous vegetation by cropping the plant so closely that it is unable to capture enough sunlight for sufficient photosynthesis and/or to reach maturity, when it produces seeds for future germination. Secondly, cheatgrass is easily dispersed by animals because the spikelet contains seeds that either easily adhere to animal hides, or may become embedded in animal hooves. With hundreds of thousands of livestock grazing the open range every year, cheatgrass was exposed to virtually every available grazing site in the Great Basin." From these studies, it appears that epizoochory, rather than endozoochory, is the primary route of cheatgrass and red brome seed dispersal by livestock.

At times, cheatgrass has been actively planted as a forage crop for livestock (Mack 1981, Peters and Bunting 1994, Mealor et al. 2013). In a bizarre twist, DeFlon (1986) promoted cheatgrass as a means of minimizing halogeton, which is poisonous to livestock. Today, cheatgrass is widely regarded as a pest species and active planting seldom, if ever, occurs.

Cheatgrass Spread by Recreational Users

Cheatgrass seeds can become embedded in mud and thereby transported on motor vehicles, including motorized recreational vehicles (Pyke 2000). Cheatgrass invades along two-track vehicle routes and, to an even greater extent, along the verges of improved and paved roadways (Gelbard and Belnap 2003). In Rocky Mountain National Park, which lacks livestock, cheatgrass is most heavily associated with roads (Banks and Baker 2011, Bromberg et al. 2011). Cheatgrass seeds readily attach to vehicle tires (and hiking shoes as well), so roads and trails are key to dispersal in Rocky Mountain National Park (West et al. 2015). Socks can also be a vector for cheatgrass transport (Mount et al. 2009).

Cheatgrass Spread through Seed Contamination

Cheatgrass seeds can be transported in contaminated seed mixes (Pyke 2000). In the 360,000 kg of grass seed applied in the first year after the Cerro Grande Fire in the Jemez Mountains of New Mexico, federal agencies inadvertently introduced over 1 billion cheatgrass seeds as part of the Burned Area Emergency Rehabilitation process (Barclay et al. 2004).

Certified weed-free hay, gravel, and straw are critical to avoid spreading cheatgrass infestations (Garner et al. 2019). Even so, cheatgrass seeds may not be precluded as part of weed-free forage or gravel standards (Pyke et al. 2016). Cheatgrass is not generally listed by local and state agencies as a noxious weed (Pyke et al. 2016).

Natural Barriers to Cheatgrass Invasion

Healthy native ecosystems provide a strong preventative defense against cheatgrass invasion. Worldwide, nature reserves are about half as susceptible to invasion of non-native plants than lands outside reserves (Lonsdale 1999). In North America, the two primary natural barriers to cheatgrass invasion appear to be robust native grasses (particularly perennial bunchgrasses), and healthy biological soil crusts. Bunchgrasses resist cheatgrass invasion, and biological soil crusts between the tussocks resist cheatgrass germination (Reisner et al. 2013). Cover of shrubs, native bunchgrasses, lichens, and mosses all are negatively correlated with cheatgrass cover (Condon and Pyke 2018). Bansal and Sheley (2016) found that cheatgrass cover was negatively associated with perennial bunchgrass cover and biological soil crust cover. Rau et al. (2014) found that native perennial grass cover was correlated with the cover of lichens and mosses that make up biological soil crust. Thus, biocrusts and perennial bunchgrasses have a synergistic, rather than simply additive, effect to resist and retard cheatgrass invasion.

Native Perennial Bunchgrasses

Colonizing species cannot successfully immigrate into stable, undisturbed sagebrush steppe habitats (Quire 2013). Perennial grasses effectively exclude cheatgrass in areas where bunchgrasses are at high density (Rayburn et al. 2014), even in areas where soil climate conditions are otherwise favorable to cheatgrass (Roundy et al. 2018). According to Mata-González et al. (2007: 153), native perennial species are superior competitors to exotic annuals in the absence of disturbance. Rosentreter (1994:172) found that "without fire, grazing, or other major disturbance, shrubsteppe habitats in good condition can exclude most exotic annuals." Perennial grasses possess high densities of roots in shallow soils, and are strong competitors with cheatgrass when they are mature (Chambers et al. 2016). Perennial grasses suppress annual grass invasions, and indeed can be the primary factor preventing cheatgrass invasion (James et al. 2008, Mazzola 2008, Davies et al. 2011a). As a result, susceptibility to cheatgrass invasion is inversely proportional to the cover of mature, native bunchgrasses (Taylor et al. 2014, Chambers et al.

2016, Williamson et al. 2019). Larson et al. (2017) found that native perennial grasses had a greater effect on cheatgrass abundance than either temperature or reduced precipitation. Reisner et al. (2013) found that three species, *P. spicata*, *A. thurberianum,* and *Poa secunda*, appear to be especially important determinants of such resistance. *P. spicata* and *A. thurberianum* are dominant deep-rooted bunchgrasses with most active growth in later spring, while *Poa secunda* is a shallow-rooted bunchgrass active in late winter and early spring. The combination of differing structure and life history strategies reflects differing abilities to access resources at different soil depths (James et al. 2008) and seasons, and limiting soil resources available to invading exotic cheatgrass. Mata-González et al. (2007: 153) concluded, "Despite its reputation for being an aggressive invader, *B. tectorum* has clear limitations to persist in a site with respect to perennials."

Bansal and Sheley (2016) found that cheatgrass was negatively associated with native species richness. However, areas with greater native species richness may not always be less susceptible to non-native plant invasion (Lonsdale 1999). Anderson and Inouye (2001) found that native species cover, but not species richness, was correlated with resistance to cheatgrass invasion. In control plots cheatgrass cover ranged from 15% to 45%, and was inversely related to cover of other understory plants and plant species richness (Keeley and McGinness 2007). Stohlgren et al. (1999) found that plant communities with high biodiversity were able to be invaded by non-native plants, and asserted that soil chemistry characteristics had more to do with vulnerability to invasion than floristic diversity. Tilman (1997) found that increasing plant diversity was correlated with decreasing invasibility in an ungrazed tallgrass prairie reserve in Minnesota. Stohlgren et al. (1999) found that invasive weeds were strongly and positively correlated with foliar cover, mean soil nitrogen percentage, and total number of exotic species. For red brome, Abella et al. (2012) found red brome presence weakly correlated with native species richness.

Cheatgrass fares poorly in black sage communities, and tends not to dominate in more mesic and cooler mountain big sagebrush communities (Miller and Eddleman 2001). Getz and Baker (2008) documented that James' galleta (*Hilaria jamesii*) was inversely related to cheatgrass cover, indicating the possibility that this grass could suppress cheatgrass, or, conversely, that cheatgrass excludes galleta. Lupines (*Lupinus* spp.), which are nitrogen-fixers, increased growth of neighboring cheatgrass and native grasses alike (Wade 2015). Precipitation in salt desert scrub appears to be too scant to support cheatgrass unless elimination of the native plants has occurred through overgrazing (Billings 1949).

Native perennials exploit water deep in the soil that is unavailable to annuals, which explains in part why undisturbed perennial plant communities exclude most exotic annuals (Rosentreter 1994). Cheatgrass has fast nitrogen uptake and large nitrogen requirements, and can be suppressed due to competition for this nutrient with native bunchgrasses (Booth et al. 2003). Chambers et al. (2007) found that cheatgrass removal or burning had a minor effect on cheatgrass emergence and survival, but biomass and seed production increased by two to three times after removal, two to six times after burning, and 10 to 30 times after removal and burning.

Undisturbed sagebrush steppe is resistant to cheatgrass invasion (Lavin et al. 2013). In an experimental setting, McGlone (2010) showed that mature perennial bunchgrasses suppress cheatgrass invasion regardless of the availability of soil water or nutrients. Anderson and Inouye (2001) found a strong negative relationship between cheatgrass and perennial grass cover. Increased cover of native shrubs and bunchgrasses and biological soil crust were all associated with reduced cover of cheatgrass and increased site resistance to cheatgrass invasion (Condon and Pyke 2018). Even at bunchgrass cover levels of only 4-8%, post-fire increases in cheatgrass were prevented when livestock were not present (Ellsworth et al. 2016). In sum, the presence of healthy and abundant native bunchgrasses forms an effective defense against cheatgrass invasion.

Biological Soil Crusts

Biological soil crusts, particularly mosses, resist cheatgrass invasion by suppressing viability of their seedlings (Root et al. 2020). Lichen-based soil crusts reduced cheatgrass seedling establishment by 85% over bare soil, while mixed crust of lichens, mosses and cyanobacteria reduced cheatgrass seedling establishment by 11% (Deines et al. 2007). Small cracks in biocrusts allow small seeds to penetrate the soil surface, but block larger seeds (like cheatgrass), which are then more susceptible to being eaten by granivores (Chambers et al. 2016). Lichen-based crusts frustrate seed germination through affecting seed water status and seedling root penetration (Serpe et al. 2008). Biological soil crusts dominated by short mosses resulted in less available moisture for seeds and significantly reduced overall seed germination (Serpe et al. 2006). Serpe et al. (2006) found that seed germination for both cheatgrass and native grass seeds was more rapid on bare ground than on moss-dominated biological soil crusts.

Bashkin et al. (2003) suggested that when soil crusts are disturbed, soil nitrogen temporarily increases and can facilitate the germination of exotic species. Conversely, trampling of soils in the Great Basin has been found to suppress seedling success for native bunchgrasses (Eckert et al. 1986). Hernandez and Sandquist (2011) documented that red brome germination was three times greater in areas where biological soil crust was physically disturbed than on undisturbed soil crust, whereas native grasses showed no difference in germination. Cattle trampling decreases biological soil crust cover, increasing sites for cheatgrass establishment (Ponzetti et al. 2007). Trampling by cattle can eliminate biological soil crusts and depress soil biota and water uptake, leading to desertification (Belnap 1995). Moderate to heavy grazing by cattle or sheep causes a major decrease in biological soil crust cover (Anderson et al. 1982b). Shinneman and Baker (2009) found that livestock-degraded sites are more prone to post-fire invasion by cheatgrass due to destruction of biological crust.

Trampled biological soil crusts may take protracted periods to recover to a natural state. Anderson et al. (1982b) found that soil crusts mostly recovered from livestock trampling within 18 years. Belnap (1995) found that livestock damage to biological soil crusts can take decades to recover, and in one case an area where trampling by livestock ceased 30 years previously, soil crusts had yet to return to full function. Algal crust components do not recover from grazing as quickly as fungal and lichen components (Anderson 1982b).

The effect of fire on biological soil crusts is equivocal, and may be mediated by disturbance. Four studies in the Basin and Range province found that fires have a negative effect on biological soil crust components, particularly lichens and mosses, while other soil crust components increased (Johansen 2001). However, in an area rested from livestock grazing, fire did not result in long-term decreases in lichens (Bowker et al. 2004).

The preponderance of studies indicate that the presence of healthy perennial grasses appears to benefit soil crust development and persistence, and vice versa. Ponzetti et al. (2007) found that biological soil crusts are positively related to native perennial bunchgrasses, and inversely related to cheatgrass. Biological soil crust cover had the greatest negative effect on cheatgrass cover in plots adjacent to roads, but had a positive relationship to native grass species (Gelbard and Belnap 2003). On the Colorado Plateau, exotic species richness and cover was positively correlated with native plant species richness and soil fertility, but negatively related to biological soil crust (Stohlgren et al. 2001). Chong et al. (2006), by contrast, found cheatgrass cover positively associated with cyanobacterial biological soil crusts. Biological soil crust species richness promotes native perennial grasses (Root et al. 2020).

Invasive plants often fill in interspaces formerly occupied by soil crusts (Rosentreter and Belnap 2001). Regarding biological soil crusts, the "first line of defense" against cheatgrass, Mack (2011: 262) stated, "Practices are needed that not only conserve these fragile organisms but also restore their role. Such restoration is problematic, given the widely varying rates of re-colonization in arid communities. … The rate of re-colonization must then be accelerated, for example by applying an inoculum of the entire cryptogamic community (not simply the species known to hamper *B. tectorum* entry directly)." Thus, maintaining healthy biological soil crusts as a land management goal will increase site resistance to cheatgrass invasion.

Climactic Factors

Climactic conditions dictate which areas are susceptible to invasion, while disturbance regime dictates the severity of invasion, and seed availability dictates the speed of invasion (Bradford and Lauenroth 2006). Higher-elevation plant communities that are more mesic tend to be more resistant to cheatgrass expansion, while lower-elevation Wyoming big sagebrush communities are highly susceptible (Reed-Dustin et al. 2016). Bunchgrass productivity increases under lower heat loads (Davies et al. 2007). Conversely, increases in soil heat load index are correlated with reduced cover of both cheatgrass and native bunchgrasses (Condon and Pyke 2018). Rao et al. (2011) found that exotic grass cover was correlated with windiness. At the drier southern edge of its range, establishment of cheatgrass and accelerated fire cycles in the Mojave Desert is more prevalent on high-elevation slopes than on low-elevation bajadas, due to greater moisture and less drought found at higher elevations, which is more conducive to *Bromus* persistence (Brooks 1999b).

Adequate precipitation appears to be a key factor in enabling cheatgrass expansion. Cheatgrass prevalence was positively associated with winter precipitation (Williamson et al. 2019). Bradford and Lauenroth (2006) hypothesized that cheatgrass outcompetes native plants only in areas with consistent water availability during autumn, winter, and early spring. Abundant spring moisture resulted in cheatgrass spread in spring-grazed pastures (Laycock 1967). Low spring precipitation results in cheatgrass mortality (Young et al. 1969).

Cheatgrass spreads more rapidly in more arid environments, but flourishes best in those areas during the years with greatest precipitation. Condon et al. (2011) found that cheatgrass cover was greatest on the driest sites. Dry summers produce dry soil conditions in autumn, requiring substantial fall precipitation to wet the soil prior to seedling establishment (Bradford and Lauenroth 2006). In a resource-poor environment, an experimental study by Mangla et al. (2011) found no evidence of competition between cheatgrass and native grass seedlings on plant biomass or survival for any species. These researchers posited that precipitation variation, where wet conditions in spring strongly favored cheatgrass and medusahead growth, and hot, dry summer conditions hampered Sandberg's bluegrass, was an overriding factor. Pilliod et al. (2017) found that cheatgrass cover was greatest in years of highest precipitation, particularly when one of the three previous years also had high precipitation. With fall precipitation, cheatgrass grows rapidly and will dominate a site by the following spring (Rosentreter 1994). Sites with higher summer precipitation showed lower cheatgrass response to fire (Taylor et al. 2014).

Miller et al. (2006) suggested that cheatgrass is water-limited in fall and spring, but nutrient limited during the winter growth season. Higher cheatgrass cover was associated with warmer late springs and warmer, wetter falls (Roundy et al. 2018). Drought is a major cause of cheatgrass mortality, particularly for seedlings (Mack and Pyke 1984). In the Mojave Desert, heavy late fall and winter precipitation were the most significant factors increasing cheatgrass (Rao and Allen 2010). Water may be limiting for cheatgrass establishment in Canyonlands National Park during fall and spring, while winter growth is limited by nutrient availability (Miller et al. 2006). Creosote scrub required exceptionally high moisture levels to produce enough cheatgrass to carry a fire (Rao and Allen 2010). However, soil water was weakly correlated with cheatgrass growth in south-central Washington, because plant growth is completed before soil water becomes limiting there (Uresk et al. 1979). Climactically, resistance to *Bromus* spp. increases as summer precipitation and total precipitation increase (Chambers et al. 2017). Nonetheless, and in contrast, one survey found that ranchers believed that drought was the largest cause of cheatgrass expansion (Kelley 2010). This paradox could be the result of timescale: If drought results in near-term reductions in cheatgrass germination and spread, yet intensifies the impact of livestock grazing on perennial bunchgrass survival, then over the long term drought-mediated suppression of perennial grasses could lead to cheatgrass spread during the wetter years that follow.

Leger et al. (2009) found that high-elevation sites are marginal for cheatgrass. Low winter precipitation and low winter temperatures do not favor the establishment of cheatgrass (Lavin et al. 2013). Cheatgrass has low establishment, biomass, and seed production and mid to high elevations due to cold temperatures and short growing seasons (Chambers et al. 2007). Mountain big sagebrush areas may even have insufficient growing degree days to support cheatgrass growth and reproduction (Chambers et al. 2007). Cheatgrass is not likely to be a strong invader at higher elevations due to soil moisture and temperature regimes, and competition from perennial bunchgrasses (Boyte and Wylie 2016). Griffith and Loik (2010) found a complex relationship between cheatgrass demographics and snow depth, with experimentally increased snow depth decreasing cheatgrass survival and seedling growth, but cheatgrass growing better during years with naturally greater snowfall.

Factors that Increase Cheatgrass Spread and Dominance

Disturbances are among several factors that can increase the likelihood, accelerate the speed, and amplify the intensity of cheatgrass invasions, disturbance by livestock and other human-caused activities chief among them (Concilio and Loik 2013, Chambers et al. 2016). Johnston (2011) projected that within 7.3 m of the edge of a disturbance, cheatgrass seedling density would exceed 40 plants per meter, enough to limit the growth of native grasses. Cheatgrass secures its foothold on areas where the natural cover has been disturbed or destroyed through overgrazing, burning, cultivation, or erosion (Warg 1938).

Bare Ground

Larger gaps between perennial plants indicate a loss or lack of perennial grasses and forbs and a corresponding increase in available resources for invading plants (Rau et al. 2014). Cheatgrass is able to colonize gaps of bare soil between bunchgrasses (Rayburn et al. 2014). Undisturbed native grasslands contain many open sites that are invasible by weed species (Tilman 1997). Historically, cheatgrass became initially established in nearly bare areas where native plant cover was deteriorated or absent (Vallentine and Stevens 1994, citing Stewart and Young 1939; Germino et al. 2016). In the Chihuahuan Desert, systems with small bare patches are considered healthy, while systems with large bare patches are considered unhealthy (De Soyza et al. 2008). Piemeisel (1951: 70) noted that invasive annuals establish where disturbance has made bare spaces, not among perennial grasses where disturbance has not occurred.

However, bare ground itself is not necessarily a determinant of invasibility. Rao et al. (2011) found that drier areas with more bare ground had greater native plant diversity, while richer soils (in areas of airborne nitrogen deposition) had greater annual weed invasion and less native plant diversity. Bare mineral soil surrounding bunchgrasses may not be invasible because the soil beneath the bare ground is fully occupied with a high density of bunchgrass roots (Tilman 1997). Adventitious roots of bluebunch wheatgrass grow laterally for 20-30 cm before turning downward, accounting for the wide spacing between nature bunchgrasses and the bare ground sometimes observed between them (Harris 1967). Further complicating the situation, temperature-moisture conditions on bare soil are frequently outside the range conducive to cheatgrass germination (Evans and Young 1970). Thus, in undisturbed areas where patches of bare ground occur naturally, these bare patches may not be susceptible to cheatgrass invasion.

Physical Disturbance

In the climactically harsh sagebrush steppe, a high rate of physical disturbance favors replacement of perennial plants by annuals, because perennials have difficulty absorbing losses year after year of being grazed (Lavin et al. 2013). Harris (1967) observed that *B. tectorum* invasion of *A. spicatum* (now *P. spicata*) only occurs after overgrazing, fire, conversion to agriculture or other disturbances. Drier sites, particularly when disturbed, are more susceptible to cheatgrass invasion than wetter, undisturbed sites (Anacker et al. 2010). Broken biological soil crusts offer microsites for weed establishment (Mack and Thompson 1982). Soil disturbance increased cheatgrass germination even more than removal of competing plants (Leffler et al. 2016). Transition of the sagebrush steppe to cheatgrass resulted from unprecedented levels of disturbance including road construction, heavy livestock grazing, oil and gas development and urbanization (Lavin et al. (2013).

Whisenant (1990: 7) observed that fire and chronic overgrazing initiates cheatgrass domination. Disturbance can increase cheatgrass invasion and dominance by reducing competition from other vegetation despite having some effect on cheatgrass germination (Roundy et al. 2007). *B. inermis* and *B. japonicus* are almost exclusively found along paved roads but not in the sagebrush steppe interior of the Idaho National Laboratory (Lavin et al. 2013). Transitions from *B. tectorum* on abandoned farm lands or heavily grazed areas is very slow (Hulbert (1955). Roads can also have lasting impacts on native biodiversity: Disturbed roadsides likely provide a conduit into small disturbed patches in the intact sagebrush steppe, but reverse colonization by native species does not take place readily into roadways and heavily grazed disturbed areas (Lavin et al. 2013).

Natural disturbances also can create microsites that support cheatgrass. Local disturbances that reduce soil compaction, such as digging by fossorial rodents, foxes, domestic dogs or coyotes, may facilitate cheatgrass expansion (Beckstead and Augspurger 2004). Rodent burrow entrances can also support cheatgrass invasion (Hulbert 1955).

Off-road vehicles may carry and disperse cheatgrass seeds (Getz and Baker 2008). Lavin et al. (2013) found that introduced species were more abundant in disturbed areas like roadsides. Cheatgrass in particular is positively associated with roads (Lovtang and Riegel 2012), and in at least one case was most prevalent along roads and in disturbed areas (Anacker et al. 2020). Dirt roads were correlated with elevated prevalence for invasive annuals in the Mojave Desert (Brooks and Berry 2006). Roads with wider disturbed verges had greater cover of cheatgrass and other weeds, and greater penetration of cheatgrass into adjacent habitats (Gelbard and Belnap 2003). In addition, physical disturbance (e.g., roads) had a much greater effect on overall plant diversity than did fire (Lavin et al. 2013). Porensky and Blumenthal (2016) found that cheatgrass had a slightly greater tendency to occur farther from roads than in close proximity in the western Great Plains. Gelbard and Harrison (2003) found that native species cover was greatest on non-serpentine soils in areas more than 1 km from roads, and least within 10m of roads. However, Shinneman and Baker (2009) found that distance to road was not a significant factor in determining post-fire cheatgrass abundance. Cattle concentrate along roadways (Getz and Baker 2008), giving cheatgrass infestations beginning along roadways a pathway to advance into unroaded habitats.

Croplands can also be a nexus for cheatgrass invasion. Cheatgrass infestations are greater on lands surrounding cultivated fields (Pyke et al. 2016). Stewart and Young (1939) noted that cheatgrass proliferates in abandoned cropfields and other heavily-disturbed areas. Abandoned alfalfa fields in the Snake River Plain subjected to moderate levels of livestock grazing or left ungrazed transitioned to Russian thistle and then to cheatgrass within two to three years (Piemeisel 1938).

Livestock Grazing

Livestock grazing is the most pervasive land use in arid and semiarid ecosystems in North America, and it is a major factor in facilitating the spread of invasive weeds (Brooks and Pyke 2002). According to Schiffman (1997: 94), humans have enabled domestic livestock to disturb soils and vegetation in ecologically unusual ways that have resulted in replacement of native plants with early succession invaders. According to Westoby et al. (1989: 268), vegetation changes resulting from domestic livestock grazing are variable, damaging, and irreversible. Hobbs and Huenneke (1992: 328) posited that a change of the species of herbivore, or an increase in the level of grazing, constitutes a disturbance. Mack and Thompson (1982: 759) observed that on the Great Plains, the introduction of cattle simply replaced bison, and areas disturbed by grazing were recolonized by native grasses and forbs, in sharp contrast to the profound changes in the Intermountain West where Eurasian weeds have replaced native vegetation. Mojave Desert plant communities are more floristically diverse, but also more fragile and slower to heal if overgrazed than the sagebrush steppes farther north (Tueller 1989). According to Zouhar et al. (2008: 25), plant communities in poor condition due to prolonged or excessive livestock grazing may show elevated susceptibility to nonnative plant invasions. Heavy grazing can effectively remove spiny hopsage and native bunchgrass, leading to dominance of cheatgrass and other weeds (Young and Evans 1975).

Livestock grazing has several significant effects on the environment. Livestock grazing in western North America causes loss of biodiversity, reduces population densities of other species, disrupts ecosystem functions including nutrient cycling and plant succession, changes biotic community organization, and changes the physical characteristics of terrestrial and aquatic habitats (Fleischner 1994, and see Kauffman et al. 2022). Cattle concentrate along streamsides, overgrazing herbaceous plants and suppressing the growth and reproduction of woody plants (Kaufmann et al. 1983, Fleischner 1994). Total belowground root biomass was 50-62% greater in riparian and wet meadow exclosures rested for 9-18 years from livestock than comparable sites

Heavy livestock grazing that that shown here in the upper Skull Valley of Utah in 2021 causes physical disturbance to soils, soil crusts, and vegetation and can functionally eliminate native bunchgrasses, leaving bare soil ideal for cheatgrass colonization. Erik Molvar photo.

where livestock grazing continued (Kaufmann et al. 2004), indicating that grazing can reduce soil carbon. Globally, grazing exclusion increases plant abundance and, over time, plant diversity (Filazzola et al. 2020). Donahue (2007) characterized livestock grazing as the single most potent agent of environmental degradation in the Intermountain West.

In addition to the obvious impacts of livestock herbivory on vegetation, livestock also impair the biodiversity of animals. Fleischner (1994) stated that the destructive effects of grazing have been documented for all vertebrate classes of wildlife. Filazzola et al. (2020) examined 109 exclosure-versus-livestock studies and determined that across most types of wildlife, livestock exclusion increased abundance and diversity of native animals, with the most striking differences occurring for native herbivores and pollinators. Detritovores were the only class of animal that decreased with livestock exclusion. Livestock grazing in riparian areas has negative effects on populations of nesting passerine birds (Taylor 1986). Excessive livestock grazing degrades sagebrush, meadow, and riparian plant communities, thereby harming sage-grouse habitats (Miller and Eddleman 2001). Monroe et al. (2017), by contrast, found that sage-grouse populations responded positively to grazing that occurred after peak vegetation productivity (May 30), but declined when heavy grazing levels occurred earlier. Small mammal populations are particularly heavily impacted by livestock grazing (Filazzola et al. 2020). Small mammal populations and species diversity were greater in ungrazed riparian habitats than in grazed habitats (Medin and Clary 1989). Sheep grazing in sagebrush steppe significantly reduces the diversity and abundance of small mammals (Reynolds and Trost 1980). According to Vavra et al. (2007: 66), ungulate herbivory has intensified in many ecosystems, as a result of adding domestic ungulate grazing pressure to pre-existing herbivory by wild ungulates, paired with the reduction or elimination of wildlife migrations and predators that previously regulated wild ungulate populations and influenced their spatial distribution. Ripple et al. (2022) found that livestock grazing was the most frequent contributor to rare species endangerment in eleven proposed conservation reserves in the western United States, with grazing cited as a threat to 48% of 92 threatened and endangered species.

Livestock grazing causes disturbance to soils and plant communities that lays the groundwork for invasive colonizers like cheatgrass. Heavy concentrations of livestock, or removal of vegetation by fire, can result in severe wind erosion and topsoil loss (Piemeisel 1938). Vallentine and Stevens (1994: 203) suggested that hoof action from cattle creates a roughened soil surface and facilitates the germination of cheatgrass through the planting action of hoof impact. According to Belsky and Blumenthal (1997: 321), livestock grazing has severely depleted native plant species, allowing weedy species to invade. Livestock grazing increases wind erosion and airborne dust, which in turn speeds snowmelt and reduces water availability in arid regions (Meyer 2011). Overgrazing can result in lowered water tables and conversion of riparian meadows to sagebrush (Wright and Chambers 2002). It is important to note that overgrazing by native herbivores also can facilitate cheatgrass invasion; Banks and Baker (2011) found that elk winter range had higher percentage of cheatgrass cover than non-winter-range, illustrating the key role of herbivory and disturbance.

Livestock import non-native seeds, and create microsites for invasion (Hobbs and Huenneke 1992). "Livestock act as vectors for seeds, disturb the soil, and reduce the competitive and reproductive capacities of native species" (Belsky and Blumenthal 1997: 321). Mealor et al. (2013) recommended holding livestock for a full week after they have grazed on lands infested with cheatgrass, before moving them to uninfested lands, to give cheatgrass seeds a chance to fully pass through the digestive tract.

According to Goodwin (1992), ecological dynamics in sagebrush grass systems were radically altered with the introduction of non-native livestock and the suppression of fire. In unburned areas, livestock grazing, and proportion of years grazed were strong positive predictors of cheatgrass occurrence and prevalence (Williamson et al. 2019). Williamson et al. (2019) examined data from 417 sites across almost a quarter million acres in the central Great Basin and concluded that grazing corresponds with increased cheatgrass occurrence and prevalence regardless of variation in climate, topography, or community composition, rejecting the hypothesis that contemporary grazing regimes or grazing in conjunction with fire can suppress cheatgrass. Most ranchers recognized overgrazing as a major cause of cheatgrass expansion in a Colorado and Wyoming survey (Kelley 2010).

Condon and Pyke (2018) found an interaction between grazing and fire that decreases site resistance to cheatgrass invasion. Rosentreter (1994) observed that most native plant species tolerate moderate grazing but even one season of overgrazing may allow invasion by cheatgrass and increased fire frequency. The effects of fire on cheatgrass invasion are clearly much greater after removal of native vegetation (Chambers et al. 2007). Regular grazing by cattle and frequent burning extend the dominance of cheatgrass (Stewart and Hull 1949). Tellingly, Taylor et al. (2014) argued that in the absence of grazing, climate rather than fire was the more dominant factor in predicting future cheatgrass cover: livestock, rather than fire, is the key factor mediating cheatgrass spread.

Cheatgrass increases in prominence with disturbance by livestock grazing and plowing (Mack and Pyke 1983). According to Piemeisel (1951), perennial vegetation can be devitalized by historical grazing to the point that it dies out even in an average precipitation year. According to Shinneman and Baker (2009), reductions in species richness and biological soil crust cover and increases in cheatgrass cover are indicators that plant communities have been degraded by livestock grazing. Idaho fescue from degraded sites showed greater reduction in growth when challenged with cheatgrass competition than did fescue from a pristine site, and ultimately adopted a shorter growth form (Nasri and Doescher 1995). Chambers and Wisdom (2009) blame the increase in cheatgrass and fire frequency on the legacy effects of past livestock overgrazing. Widespread and intensive grazing by cattle and sheep introduced large-scale, widespread disturbance that facilitated the dominance of invasive bromes and other weeds in California grassland systems (Schiffman 1997). Robertson and Kennedy (1954) attributed the appearance of cheatgrass in northeastern Nevada to a large influx of domestic sheep from Bakersfield, California. Sparks et al. (1990) documented shifts from perennial bunchgrasses in shadscale and sagebrush habitats to cheatgrass near the Dugway Proving Ground between the 1870s and modern times, caused by poorly managed livestock grazing and fire.

According to Mack and Thompson (1982), the demise of all forms of North American wheatgrass is due to a lack of prior adaptation to grazing by ungulates. Mazzola (2008:8) added, "Initial invasion of *B. tectorum* is often facilitated by removal of perennial grasses due to overgrazing by livestock." Biomass removal, simulating grazing, increased cheatgrass density only briefly for areas dominated by native bunchgrass (McGlone et al. 2010). Mealor et al. (2013) observed that perennial plants that are continuously overgrazed cannot compete with cheatgrass. Young and Clements (2007) observed that repeated, widespread grazing at the wrong season facilitated dispersal and community dominance by cheatgrass on Nevada rangelands.

A few researchers have asserted that the role of livestock is not definitively tied to cheatgrass spread. Davies et al. (2011a) argue that livestock grazing either has limited impact on cheatgrass spread or a beneficial effect in reducing cheatgrass expansion. In the context of old-field succession on the Snake River Plain, Piemeisel (1938) argued that heavy livestock grazing retards cheatgrass establishment and favors the annual weeds Russian thistle (*Salsola tragus*) and tumble mustard (*Sisymbrium altissimum*) instead. Clements (2007) argued that while improper livestock grazing accelerated the spread and dominance of cheatgrass, this spread would have occurred, albeit at a slower pace, even without livestock. These differences may be due to the degree and intensity of grazing and the mild moisture regime in central Oregon versus the harsher and more arid Snake River Plain of Southern Idaho.

Livestock grazing can cause deterioration of the ecosystem through removal of long-lived perennial grasses (De Soyza et al. 2008). Heavy livestock grazing depletes native bunchgrasses and increases cheatgrass cover (Pickford 1932). Young et al. (1972) described the effect of a century of domestic livestock on western perennial grasses as one of gradual attrition. Beckstead and Augspurger (2004) found that reducing native grasses resulted in increased cheatgrass density. According to Reisner et al (2013:1), "Grazing exacerbates *Bromus tectorum* dominance in one of North America's most endangered ecosystems by adversely impacting key mechanisms mediating resistance to invasion." Defoliation by herbivores exposes the growing points of native bunchgrasses to thermal damage, leading to increases in invasive species (Carter et al. 2014). According to Knapp (1996), livestock grazing in the Great Basin was devastating to the native grasses, unlike on the Great Plains where cattle replaced bison with little ecological impact. In an experiment simulating livestock grazing, Britton et al. (1990) found that both burning and clipping (simulating livestock grazing) reduced the basal area of native bunchgrasses, with some grasses demonstrating greater responses to either burning or clipping than others. The effect of grazing and fire on native grasses can be additive. Biomass and seed production of cheatgrass increased two to three times following removal of native herbaceous vegetation, two to six times after burning, and 10-30 times following removal (an experimental surrogate for grazing) and burning (Chambers et al. 2007). Removal of grasses and forbs accelerated cheatgrass spread more than removal of sagebrush (Leffler et al. 2016).

Grazing by ungulates suppresses palatable forage species, conferring competitive advantage to unpalatable invasive species (Vavra et al. 2007). Cattle herbivory alters bunchgrass community composition by favoring grazing-resistant species while suppressing grazing-intolerant species, and ultimately decreases bunchgrass abundance (Briske and Richards 1995). Western lands dominated by perennial bunchgrasses under natural conditions have instead been converted, primarily through overgrazing, to annual grasslands susceptible to invasion by introduced forbs (DiTomaso 2000). In sagebrush ecosystems, removal of perennial species due to overgrazing and the increase in soil resources, particularly in the upper soil layers, may be a leading cause of invasion by annual grasses (Chambers et al. 2007). Root growth in grazing-tolerant grasses ceases after 50% of the aboveground shoots are removed (Briske and Richards 1995). Cottam and Evans (1945) found that weed density was twice as great in a heavily-grazed canyon as in a nearby ungrazed canyon, while density of palatable species was one-fifth as great in the heavily-grazed canyon. Reisner (2010) found that cattle herbivory was

Above: *The Bureau of Land Management built an exclosure near Contact, Nevada excluding livestock here in 2016; as of 2023 when this photo was taken, native bunchgrasses are abundant.* ***Below:*** *Just outside the exclosure, lands grazed by cattle have a cheatgrass-dominated understory with few if any native bunchgrasses in the understory. Erik Molvar photos.*

bunchgrasses, shifts in bunchgrass composition favoring the most grazing-tolerant species, and bunchgrasses being limited to protected areas beneath shrub canopies which livestock had difficulty reaching. Grazing decreases plant longevity (Briske and Richards 1995).

Adaptations of Cheatgrass to Heavy Grazing:

Cheatgrass has multiple ways of escaping damage from livestock grazing. Cheatgrass is able to develop prostrate tillers after multiple grazing occurrences that place their seeds below the lowest level of grazing for many livestock (Pyke et al. 2016). Cheatgrass has sharp awns (Upadhyaya et al 1986, Knapp 1996, Young and Allen 1997, Kaczmarski 2000, Mealor et al. 2013) and low palatability (Stewart and Hull 1949, Cook and Harris 1952, Murray et al. 1978), when dry and dead, that discourage herbivory. After this annual grass dies, cheatgrass escapes damage from herbivory by dying (in contrast to native perennial grasses, which rely on surviving as adult plants), and seeds dropped prior to grazing can escape damage to sprout the following spring.

Livestock grazing increases susceptibility of Wyoming big sagebrush ecosystems to cheatgrass invasion by trampling biological soil crusts and suppressing native bunchgrasses (Reisner et al. 2013), the two strongest natural defenses against cheatgrass. Livestock grazing can interact with drought to facilitate major cheatgrass expansions. McGlone et al. (2009) found that heavy grazing on drought-stressed perennial grasses facilitated an expansion of cheatgrass by creating vacant niches that cheatgrass seedlings could exploit. By removing perennial forbs and grasses, grazing results in significantly greater soil water and nitrogen availability (Chambers et al. 2007, Leffler et al. 2016). With increasing cattle grazing intensity, cheatgrass increases while forbs and native bunchgrasses decrease (Reisner et al. 2013). Consistent with other studies (Chambers et al. 2007; Prevey et al. 2010), Reisner et al. (2013) found that bunchgrasses reduced the magnitude of *B. tectorum* invasions, most likely by reducing water and nutrient availability.

Spring grazing by domestic sheep in salt-desert shrublands results in shrub losses and an increase in cheatgrass (Laycock 1967, Kitchen and Hall 1996). Factors that deplete perennial bunchgrasses like livestock overgrazing or infilling by pinyon or juniper trees decrease resistance to weed invasion and decrease resilience following fire (Brooks and Chambers 2011).

Cheatgrass impacts are greater in the Mojave and Basin and Range provinces than on the Great Plains (Germino et al. 2016). In the Mojave Desert, alien species comprised only 6% of the annual species during high-rainfall years, but made up 66% of the annual plant biomass (Brooks and Berry 2006). According to Meyer (2011:1), “The elimination of perennial understory vegetation and cryptobiotic crusts is a nearly inevitable consequence of livestock grazing in deserts. This opens these systems to annual grass invasion, subsequent burning, and loss of a major carbon sink, a heavy price to pay for the minimal economic gains derived from direct use of these intrinsically unproductive lands for livestock production.”

There has been a longstanding suspicion that heavy livestock grazing causes the expansion of woody plants, as competing grasses are suppressed. Blaisdell (1953) and Young et al. (1972) asserted that heavily-grazed sagebrush rangelands resulted in more sagebrush at the expense of perennial grasses. However, Vale (1975) found that shrubs were abundant prior to the introduction on livestock in North America, so brush abundance is not necessarily evidence of overgrazing. Cheatgrass competition with sagebrush increases with increasing livestock grazing pressure (Reisner et al. 2015), to the detriment of the shrub. Condon and Pyke (2018) found that shrub cover was reduced on sites with higher historical grazing pressure. Sagebrush facilitates the survival of native bunchgrasses under shrub canopies in the face of heavy livestock grazing and cheatgrass invasion (Reisner et al. 2015). Thus, the loss of sagebrush reduces the ability of perennial bunchgrasses to persist.

Livestock grazing also tips the balance toward cheatgrass in pinyon-juniper woodlands. In burned pinyon-juniper woodland on the Uncompahgre Plateau of western Colorado, the area with highest livestock use had the greatest cheatgrass cover post-fire (Getz and Baker 2008). The addition of fine fuels to the understory can make these woodlands more fire-prone.

Biological soil crusts are heavily damaged by livestock grazing through direct soil compaction. Ponzetti and McCune (2001) found that biological soil crust species were more abundant and diverse inside livestock exclosures than in grazed areas.

Yeo (2005) also found that ungrazed areas had significantly greater biological soil crust cover. Grazing intensity also plays a role. Root et al. (2020) found that plots with the lowest grazing intensity averaged 46% biological soil crust cover, versus 7% cover for plots with the highest grazing intensity. Belnap et al. (2006) observed that soil crust species richness was unaffected by cheatgrass in areas never grazed by livestock, but areas with past intermittent livestock grazing showed a lower species richness in soil crust biota. Trampling intensity determines the degree of soil crust disruption, with impacts ranging from imperceptible at very light grazing intensities, to disappearance at heavy grazing intensities, and in particular decimation of soil crusts near water sources (Warren and Eldridge 2001). Domestic sheep create more soil disturbance through hoof action and total hoof pressure than do cattle on an AUM-for-AUM basis (Condon and Pyke 2018). Grazing in winter and early summer can be particularly detrimental to soil crusts due to low soil water content at these times, but soil crusts are protected by snow and frozen conditions during winter (Warren and Eldridge 2001). Rest from livestock grazing allows biological soil crusts to recover over time (Kaltenecker et al. 1999). To protect soil crusts, "Destocking will most likely be required during periods of prolonged drought" (Warren and Eldridge 2001: 411). Damage to soil crusts has immediate implications for cheatgrass infestations: Belnap (1995:50) found that invasive grasses were much more common in trampled vs untrampled areas. St. Clair et al. (1984) found that perennial bunchgrasses showed superior rates of seedling establishment on undisturbed biological soil crusts than on crusts that had experienced simulated trampling by livestock.

Due to the propensity of post-fire grazing to accelerate cheatgrass expansion, it has become common practice on public lands to rest burned sites from livestock grazing for two growing seasons (at least 1.5 years) or more after fire. Miller et al. (2014) recommend resting burns or vegetation treatments for at least 2 years following treatment, and longer where resilience is low, treatment intensity is high, or annual grasses are dominant or co-dominant. West and Hassan (1985) recommended a few years of livestock exclusion following fire to allow grasses to recover. Severe grazing following fire further reduces the vigor of native grasses at drier sites, leading to mass cheatgrass invasion (Stewart and Hull 1949). Burned sites experience increased subsequent grazing pressure based on post-fire dung density, which was correlated to greater cheatgrass cover (Condon and Pyke 2018). According to Stewart and Hull (1949: 68), "Grazing animals … congregate on burned-over areas as soon as they become green. This accentuates and sharpens the acute stress to which perennial grasses are put on burned-over cheatgrass ranges. The final result is the disappearance of perennial vegetation and a badly exposed soil, which because of destruction of litter and loss of perennials is less permeable and highly susceptible to erosion." Brooks (2008b) recommended the temporary closure of burned areas to people and livestock to reduce seed import. Young et al. (1987) advocated for resting burned areas for two years post-fire to allow native grasses to recover.

High Plains grasslands, characterized by sod-forming grasses that evolved with intermittently heavy bison grazing, exhibit a different relationship with cheatgrass and other *Bromus* species. Stohlgren et al. (1999) found no consistent relationship between fire or livestock grazing and cheatgrass on the High Plains and Rocky Mountains. Nonetheless, Prevéy and Seastedt (2015) reported that cheatgrass is increasing on the shortgrass prairies of the Colorado Front Range.

Grazing reduces site resistance to cheatgrass invasion independent of fire (Condon and Pyke 2018). Concilio and Loik (2013) found that cheatgrass dominance and cover overall were greatest on grazed, burned plots versus other treatments. Condon et al. (2011: 602) found that juniper woodlands subjected to high-intensity fire had low perennial bunchgrass cover because inappropriate livestock grazing prior to the fire, combined with post-fire grazing, suppressed recovery of native perennial grasses. The propensity for livestock grazing to suppress or even eliminate native perennial grasses has led range managers to label these species "decreasers." Concilio and Loik (2013) found that abundance of perennial bunchgrasses that are preferred forage species were lowest in grazed compared to ungrazed plots in all years except one. Full recovery following a single event of heavy defoliation can take six years for Idaho fescue and eight to ten years for bluebunch wheatgrass (Mueggler 1975).

While rotational grazing has been proposed as a cure-all for land-health problems, it creates the very conditions that exacerbate cheatgrass expansion, and has been largely discredited by the scientific community (e.g., Briske et al. 2013). Willms et al. (1990) found that Savory-style high-intensity, short duration grazing leads to long-term range deterioration and loss of native bunchgrasses. According to Carter et al. (2014:1), livestock grazing under this "holistic" method is as detrimental to plants, soils, water storage, and plant productivity as conventional grazing systems. High-density, short-duration grazing resulted in 44.4% more soil compaction than low-density rotational grazing, contrary to the claim that hoof action breaks the soil crust and that large deposits of dung and urine increase soil nutrients (Chamane et al. 2016). Olff and Ritchie (1998: 263) observed that "large herbivores at high density, such as in intensive livestock grazing, can graze unselectively and/or create widespread erosive, detrimental soil disturbances, leaving only a few tolerant plant species, thus reducing plant diversity."

DeFlon (1986: 17) contended that domestic sheep may be particularly effective at promoting cheatgrass spread: "We have found that running sheep without overgrazing will increase the amount of new [cheatgrass] the following spring. We believe their small hooves punch the seed in the ground and till the soil at the same time, thus aerating the soil and preparing a preparing a seed bed." "While sheep and cattle competed for many of the same resources, the impact of the sheep on the landscape was probably even greater than that of the cattle," observed Knapp (1996). In northeastern Idaho, Seefeldt and McCoy (2003) found that spring grazing by sheep increased annual grasses, while fall sheep grazing increased perennial grasses; ungrazed plots had the lowest cover of invasive annual grasses.

Cattle concentrate near water in sagebrush steppe settings, and grazing intensity decreases with distance from water (Adler et al. 2005). Livestock can create gradients of intensive damage around watering sites called "piospheres," up to and including denuded zones, that can be hotspots for invasive species establishment, and native plants tend to be depressed by this level of impact (Brooks et al. 2006). As a result, areas near water tanks can support dense populations of invasive annuals (Brooks and Pyke 2002). For piosphere areas, Condon and Pyke (2018) observed, "Livestock hoof action likely broke up biocrusts, and killed perennial plants, while also working *B. tectorum* seed into the soil providing safe sites for establishment." Alien annual grass cover increased, while native plant cover decreased, with increasing proximity to watering sites (Brooks et al. 2006).

Cheatgrass can colonize undisturbed rangelands, but remains at low density in this setting (Young and Allen 1997). *Bromus spp.* that invades undisturbed areas typically do so at subdominant levels, typically achieving less than 20% of vegetation cover (Germino et al. 2016). Cheatgrass has been documented in near-pristine communities such as kipukas isolated from livestock in the midst of old lava flows (Tisdale et al. 1965, Young et al. 1972). However, healthy and undisturbed vegetation can serve as a firewall against cheatgrass spread. Piemeisel (1951) found that mature sagebrush communities adjacent to cheatgrass that were protected against rabbit and livestock use were not penetrated by the cheatgrass. Vallentine and Stevens (1994) concluded that livestock grazing enables and promotes the establishment and prominence of cheatgrass on western rangelands. Young and Allen (1997) found that excessive spring grazing, when repeated, weakens native perennial grasses and promotes cheatgrass increase. Condon and Pyke (2018) found that neither grazing nor fire directly affected cheatgrass cover, but both affected cheatgrass indirectly by suppressing native grasses and biological soil crusts.

A handful of studies dispute the central role of livestock grazing in mediating the spread of cheatgrass. Reid et al. (2008) argued strenuously against the primary role of livestock in laying the groundwork for cheatgrass invasion, proposing that livestock grazing only accelerates inevitable cheatgrass invasion by a few decades. It is difficult to measure current grazing pressure due to inconsistencies within and among agencies in measurement of livestock allocations (Condon and Pyke 2018); native bunchgrass cover was positively associated with past fire in this study, but negatively associated with grazing intensity. However, the bulk of the research suggests that the role of livestock in increasing the spread and severity of cheatgrass infestations is one of direct causation.

Livestock grazing is effectively the ecological switch that tips grass dominance in the interspaces between shrubs from native bunchgrasses to cheatgrass (Reisner et al. 2015). According to Harris (1967: 89), "Largely through economic pressures and a general lack of understanding, intensified grazing resulted in widespread destruction of *A. spicatum* [bluebunch wheatgrass, now *P. spicata*] and an opportunity for weed invasion on a grand scale." In California, exotic annual grasses were not superior competitors to native grasses for light, nitrogen, phosphorus, or water, but instead livestock grazing was the key ecological trigger that enabled exotic grasses to dominate (HilleRisLambers et al. 2010). The findings of Bansal and Sheley (2016) suggest that short-term impacts of grazing on cheatgrass may be weak, but long-term, cumulative impacts of grazing on suppressing perennial grasses may be a long-term driver of cheatgrass expansion. Bunchgrass abundance is inversely related to the size of and connectivity between gaps in perennial vegetation (Herrick et al. 2005). Increases in the size and connectivity of these gaps are associated with a dramatic increase in the magnitude of cheatgrass invasions, due to increased soil resource availability (James et al. 2008, Okin et al. 2009). Under heavy livestock grazing, native perennial grasses disappear from the inter-shrub spaces, which then become dominated by cheatgrass, but native grasses are able to persist beneath the canopies of individual sagebrush plants (Reisner et al. 2015). Hosten and West (1994: 61) found higher cheatgrass densities in burned treatments, and attributed this to fire being an acute disturbance (involving total removal of foliage) compounding the chronic disturbance of livestock grazing (partial removal of grasses over time). In the absence of livestock grazing, by contrast, incidence and cover of cheatgrass do not increase following fire (Taylor et al. 2014).

There is a current trend to identify cheatgrass invasion as an artifact of historical livestock grazing, denying that current levels of livestock grazing play a role in current increases in cheatgrass extent and severity. Several researchers (Rice et al. 2008, Pyke et al. 2016, Condon and Pyke 2018) attribute the spread of cheatgrass across the West to severe historic overgrazing, but concede that there is a lack of current data to assess the influence of current livestock grazing on cheatgrass-perennial dynamics. Epanchin-Neill (2009) points out that past cattle grazing was often heavier than current, more regulated grazing, implying that cheatgrass invasion may be a historical artifact. It is well documented that widespread overgrazing by cattle and sheep after white settlement reduced competition by native grasses and forbs (Chambers et al. 2007: 118). In one study, heavier historical grazing pressure was correlated with increased cheatgrass cover (Condon and Pyke 2018), while current grazing showed no effect. Likewise, Pendleton et al. (2013) argued that heavy grazing by livestock was damaging to Mojave Desert ecosystems, but that current levels of grazing were unlikely to cause significant damage. However, the intensity of livestock grazing is inconsistently quantified across the West, rendering comparisons between areas difficult (Fleischner 1994), even where soils and ecosystems are similar.

It is clear that the range and dominance of cheatgrass increased dramatically during the late 1900s (Monsen 1994), indicating conditions during the latter part of the last century have continued to contribute to cheatgrass' continued and accelerating spread. These observations, paired with the major acreage increases documented here and spanning the past three decades (Figure 5), point to livestock grazing's role in spreading cheatgrass infestations as an ongoing, rather than merely historical, phenomenon. Regarding livestock grazing, Fleischner (1994: 636) said, "While undoubtedly there are exceptions to this theme of destruction, clearly much of the ecological integrity of North American habitats is at risk from this land management practice."

Vegetation Manipulations or Modifications

Vegetation projects, targeting sagebrush or pinyon-juniper woodlands, pose a risk of becoming significant hotspots of cheatgrass invasion. Land management agencies have frequently engaged in large-scale vegetation manipulations, chiefly with a goal of increasing the forage available to livestock. Chaining pinyon-juniper woodlands results in a short-term increase of understory forage plants, including grasses and shrubs, but these decline as trees re-establish dominance on the site (Tausch and Tueller 1977).

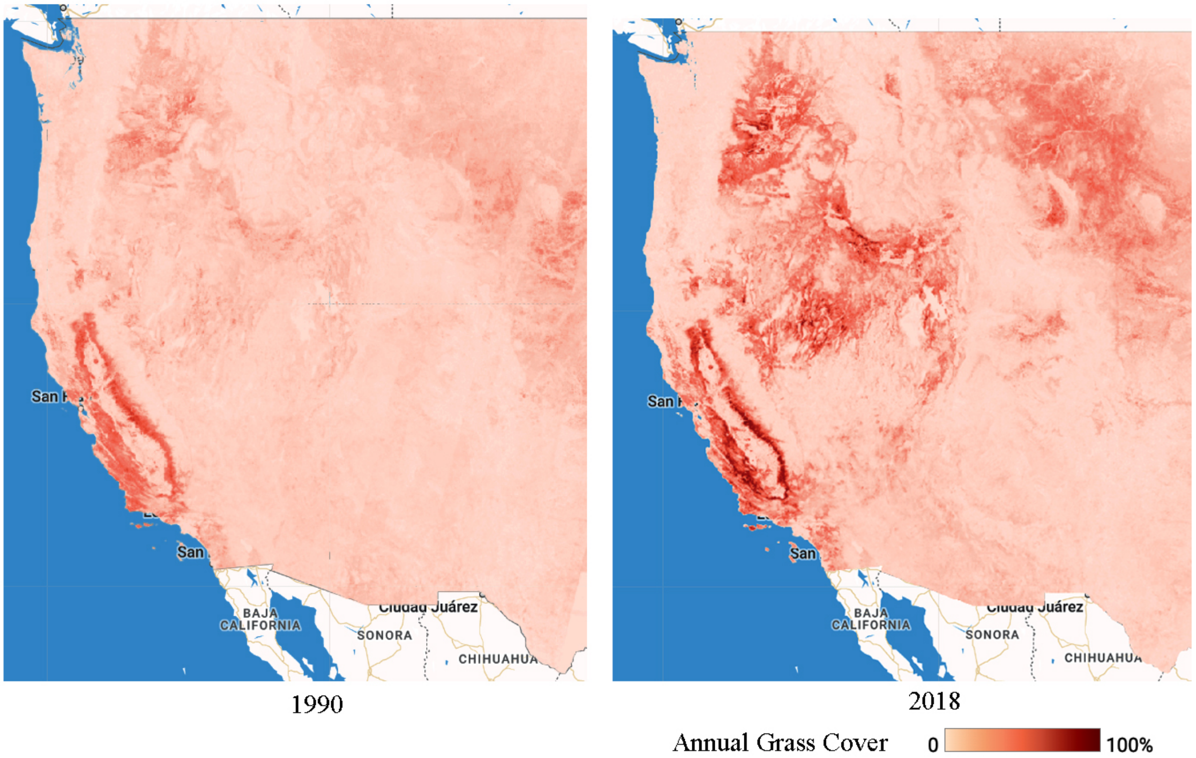


Figure 5. Difference in annual grass cover between 1990 (at left) and 2018, demonstrating continued expansion of cheatgrass. Reproduced from the USDA Rangeland Analysis Platform.

With livestock excluded, juniper removal promotes a nine- to twelvefold increase in herbaceous productivity (Bates et al. 2005).

Wisdom and Chambers (2009) posit woodland expansion (by native trees) as an ecological threat in the West. Condon et al. (2011) suggested targeting juniper woodlands for mechanical removal where they occupy more mesic, productive sites with high cover of perennial grasses in the understory. Davies et al. (2011a) argued that priority should be placed on restoring areas in the early stages of conifer encroachment. Ricca and Coates (2020) promote juniper removal to improve sage-grouse habitats. However, juniper expansions and contractions have occurred naturally for millennia in the West (Miller and Wigand 1994) and juniper removal areas may not return to a shrubsteppe state for many years (Bates et al. 2005).

Exotic annual grasses can be a threat after conifer control (Davies et al. 2011a). Cheatgrass presence is associated with juniper presence and with fewer trees per acre, according to the findings of Lovtang and Riegel (2012). Mechanical mastication of junipers in treatment areas promotes the growth of both cheatgrass and perennial bunchgrasses through increasing soil nitrogen, so the relative abundance of each prior to the project determines the post-treatment grass community (Young et al. 2013). Mastication of juniper resulted in an increase in cheatgrass cover across all tree cover classes, likely as a result of increased soil resource availability, which favors invasive species (Bybee 2013). In sites at high risk of cheatgrass conversion, use of fire or mechanical treatments to eliminate pinyon or juniper woodlands may enhance cheatgrass invasion (Wisdom and Chambers 2009). Post-treatment risk of cheatgrass dominance is greatest where cheatgrass is a large component of the pre-treatment vegetation (Bybee 2013). If perennial grasses have been weakened or lost in juniper woodlands, and cheatgrass is prevalent, then cheatgrass is likely to expand following juniper treatments (Young et al. 2013). Seven years after killing of mature junipers, cheatgrass dominated one northern California site (Evans and Young 1985). Hamilton et al. (2019) found that cheatgrass density almost doubled as a result of conifer removal using hand-cutting with burning and chipping, and seeding with native grasses. Thinning and burning projects in ponderosa pine forest of the Uinkaret Mountains of northern Arizona resulted in a 90-fold increase in cheatgrass cover over a seven-year period (McGlone et al. 2009). Data gathered by McGlone et al. (2009) suggest that small-diameter ponderosa pine thinning in combination with drought and grazing exacerbated cheatgrass spread.

Treatments in mature to old-growth pinyon-juniper woodlands pose the greatest risk of cheatgrass infestation. Roundy et al. (2014) found that pinyon-juniper removal across four Great Basin states resulted in an increase of cheatgrass on treated sites, at all tree densities after burning, and at moderate to high tree densities for mechanical treatments. Herbicide treatment using 2,4-D to remove shrubs can result in domination of the site by cheatgrass in a similar manner to (Young et al. 1972). Once pinyon-juniper cover reaches 60-80 percent, understory shrub cover approaches zero (Bybee 2013), and fire tends to result in site invasion by invasive annual grasses (Swanson and Gilgert (2009). *B. tectorum* yield under the canopies of herbicide-killed mature junipers increased from essentially zero to 1,400 kg/ha within four years of the herbicide treatment (Evans and Young 1985). For post-treatment pinyon-juniper mastication sites, cheatgrass cover was highest for sites with the highest initial tree cover (Bybee 2013). In the absence of livestock, cheatgrass increased during the fourth through sixth years following juniper removal, but gradually declined (Bates et al. 2005).

Response of cheatgrass to mechanical treatments varies by site, and is heavily influenced by the abundance of perennial grasses and cheatgrass on the pre-treatment site (Roundy et al. 2018). Tree removals in areas already invaded by cheatgrass have a higher risk of cheatgrass dominance post-treatment (Roundy et al. 2014). Driscoll (1964) found cheatgrass associated with juniper trees, even after long rest from livestock grazing, occupying the shady areas under the north and east sides of the tree canopy. Pinyon and juniper removal in Great Basin National Park failed to increase native herbaceous plant density, but did cause a large increase in cheatgrass (Hamilton et al. 2019). According to Lovtang and Riegel (2012: 90), thinning, burning, and mowing can cause cheatgrass to invade or increase. Conifer treatments should be prioritized in areas with minimal risk of exotic grass invasion (Davies et al. 2011a). Tree removal treatments should be limited to areas where perennial grasses are healthy and abundant, before biotic thresholds are crossed (Roundy et al. 2014). A pre-treatment density of 2 to 3 perennial bunchgrass plants per meter was found to be sufficient to permit natural recovery following juniper removal (Bates et al. 2005).

Herbicide treatments targeting sagebrush may or may not result in significant cheatgrass expansion. Sagebrush thinning using the herbicide tebuthiuron resulted in a significant expansion of cheatgrass in the Wyoming Basins ecoregion, and conditions favorable to cheatgrass extended on for years (Blumenthal et al. 2006). In contrast, Rau et al. (2014) found that tebuthiuron treatments had the lowest levels of cheatgrass expansion, possibly because sagebrush die slowly, creating less of a pulse of available water and nutrients for cheatgrass.

Climactic Conditions

Sites with drier, hotter climates appear to be more susceptible to cheatgrass invasions, although red brome seems to be more prevalent in the hottest regions. In the Mojave Desert, cheatgrass is not found in great density below 4,000 feet (Hunter 1991). Taylor et al. (2014) suggested that the positive feedback loop between cheatgrass and fire is more prevalent on sites with higher temperatures and lower summer precipitation. Higher heat loads and spring insolation increase cheatgrass abundance (Stewart and Hull 1949; Chambers et al. 2007). Cheatgrass cover increases with increasing temperature and aridity (Bansal and Sheley 2016).

Notwithstanding the greater vulnerability of arid lands, abundant precipitation is favorable for much greater biomass production of cheatgrass (Stewart and Young 1939). Wade (2015) found that cheatgrass has a more pronounced response to increased spring moisture than did native grasses. Cooler and wetter conditions were associated with increased cheatgrass cover after fire (Shinneman and Baker 2009). Cheatgrass biomass was lowest during the driest years, and greatest during the years with the most precipitation (Concilio and Loik 2013). On a site with soils of low-nitrogen-fixing potential, cheatgrass cover decreased to near zero during droughts, but increased rapidly during wet periods; perennial grass cover remained stable during drought (West and Yorks 2002). Wade (2015) noted that variability in precipitation from year to year had a stronger effect on cheatgrass than on native species, depending on specific conditions.

Elevation and aspect can also play significant roles. Cheatgrass seldom occurs in abundance above 6,000 feet (Warg 1938). Cheatgrass in the northern Great Basin averaged less than 2% cover at altitudes between 5,740 and 6,500 feet, compared with almost 9% at altitudes below this threshold (Boyte and Wylie 2016). Winter death of cheatgrass is commonly caused by frost-heaving in frozen soils (Mack and Pyke 1984). Cheatgrass is capable of rapid population growth at high elevations (Griffith and Loik 2010). Cheatgrass expansion following fire may be greater on south-facing slopes than on north-facing slopes (Reed-Dustin et al. 2016). Mid- to low-elevation sites have a greater chance of ignition than high-elevation sites due to greater flammability from greater CO_2 concentration (Blank et al. 2006). Cheatgrass is more likely to be present at lower elevations in the central Great Basin (Williamson et al. 2019). In a study area not grazed since 1970, Davies et al. (2012b) found that low-elevation sites were dominated by sagebrush heavily invaded by cheatgrass prior to the first of two fires; mid elevation sites showed less cheatgrass invasion, and more patchy response to fires, while high elevation sites were most resilient.

Inherent Differences in Vulnerability of Plant Communities to Cheatgrass Invasion

Wyoming sagebrush (*A. tridentata subsp. wyomingensis*) are the most common sagebrush communities on lower, more arid sites, but are the least resistant to invasion by annual plants and the least resilient to disturbance (Miller et al. 2011, Chambers et al. 2014). Even in the absence of fire, these communities are especially vulnerable to invasions by cheatgrass, which can ultimately dominate the herbaceous understory communities (Miller et al. 2011). Resistance to cheatgrass invasion is highest for mountain big sagebrush and mountain shrub ecotypes, and lowest for salt desert scrub and Wyoming big sagebrush steppe (Wisdom and Chambers 2009).

Concilio and Loik (2013) found that cheatgrass cover was negatively correlated with plant biodiversity, but found no relationship between cheatgrass and native grass density and richness. After five years of cheatgrass invasion, invaded plots showed a significant reduction in native species richness, including a loss of ecologically important nitrogen-fixing and nectar-producing species (McGlone 2010). Cheatgrass invasion is more rapid and severe in C_4 than in C_3 communities, possibly due to higher nutrient availability (Schaeffer et al. 2012). Stohlgren et al. (2001) noted that high total plant cover may be a result of favorable growing sites, and high crust cover could be indicative of sites with less livestock-related disturbance or flooding. These researchers found that exotic plant species were more prevalent in washes than in upland sites.

Both sagebrush and bitterbrush harbor moderate microclimates beneath their canopies, supporting greater densities of cheatgrass than in intershrub spaces (Griffith 2010). Shrubs also provide favorable microsites for native grass and forb seedling establishment, and influence the pattern of snow accumulation and retention (Rosentreter 1994). In invaded communities, bunchgrasses become established beneath shrubs due to greater availability of soil moisture, and the elimination of shrubs further impairs bunchgrass establishment (Mazzola 2008). Meyer et al. (2001) found that cheatgrass establishing in shrub clumps had greater growth and seed production, and that shrubs served as "nurse plants" for cheatgrass; the death of shadscale shrubs resulted in even greater cheatgrass expansion due to release from competition.

Cheatgrass in Forested Environments

Cheatgrass appears to be shade-intolerant. Mack (2011: 258) used both glasshouse and field experiments to establish that cheatgrass is an open habitat plant that is severely shade intolerant. Cheatgrass tends not to grow in montane coniferous forests, or in riparian habitats with saturated soils (Lovtang and Riegel 2012). Pierson and Mack (1990) reported that cheatgrass survives poorly in coniferous forests, and has depressed seed production in these areas because it cannot tolerate a dense forest canopy. In addition, conifer duff suppresses cheatgrass germination (Gundale et al. 2008). Pine and spruce extracts completely inhibited the germination of cheatgrass seeds

(Machado 2007). Rice and Mack (1991) attributed dispersal of cheatgrass to livestock moving from infested sage-steppe habitats to forest clearcuts during the summer. Janzen (1994: 340, references omitted) observed that cheatgrass incursions into woodlands is heavily dependent on human-caused disturbances.

In ponderosa pine savannahs, soils beneath pine canopies are rich in nitrogen and phosphorus, and after a fire support a dense growth of cheatgrass around the base of the tree (Gundale et al. 2008). This dense growth disappears within 5 to 10 years in the absence of fire as duff builds up beneath the tree. When fires consume the duff that inhibits cheatgrass germination, and create a pulse of inorganic nitrogen, these factors in concert with the inherent phosphorous abundance beneath ponderosa pine canopies create ideal conditions for cheatgrass growth (Gundale et al. 2008). In ponderosa pine woodlands in Arizona, fires increased cheatgrass cover from less than 0.5% to 3% in moderate-severity burns and 19% in high-severity burns (Crawford et al. 2001). Under these conditions, frequent ground fires that maintain a savanna aspect of ponderosa woodlands might be expected to keep these areas more resistant to cheatgrass than infrequent, high-intensity fire regimes.

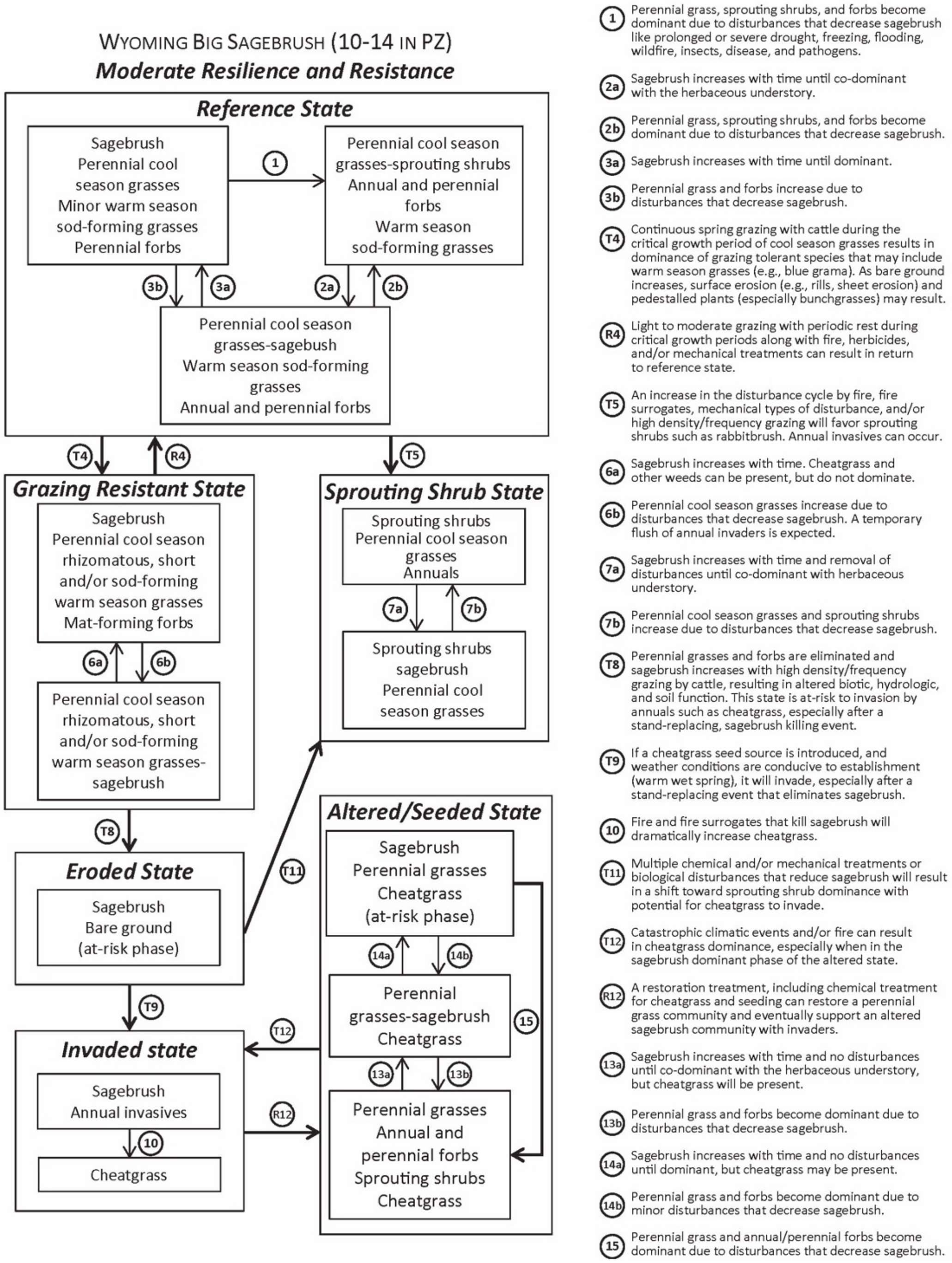
The State-and-Transition Model of Cheatgrass Invasions

Westoby et al. (1989) proposed state-and-transition modeling as an alternative to traditional plant succession. Under state-and-transition models, the outcome of the grass/fire cycle is a transition from perennial plant communities to exotic annual grasses, an alternative stable state from which it is difficult if not impossible to redirect the plant community back to native perennials (Shinneman et al. 2018). Once a critical "tipping point" is reached, ecosystems can transition to an alternate state from which return to the original state is very difficult and unlikely in the absence of human intervention (Stringham et al. 2003, Scheffer et al. 2009, Brooks and Chambers 2011). According to the Western Association of Fish and Wildlife Agencies (WAFWA 2015), unchecked invasion by annual invasive grasses will lead to a state transition in sagebrush systems reinforced by a fire cycle that perpetuates annual weeds on the landscape to the detriment of wildlife and human endeavors.

Young and Evans (1978) characterized rapid state transition in sagebrush habitats as irreversible and attributed to livestock grazing and invasive annual plants. Bagchi et al. (2013) proposed two states for sagebrush steppe ecosystems: sagebrush with bunchgrass, and cheatgrass. According to Klemmedson and Smith (1964: 237), most researchers of the time agreed that prior disturbance is generally a prerequisite to cheatgrass invasion. Crawford et al. (2004) proposed a state-and-transition model adapted from West (1989) in which livestock grazing suppressed bunchgrasses and increased annual grasses, which through fire transitioned ultimately to annual grass monocultures. Likewise, Boyd et al. (2014) proposed a state-and-transition model in which native sagebrush communities could be converted to an understory of cheatgrass and Sandberg's bluegrass, which could then be converted by fire to cheatgrass monoculture with frequent fire. Brooks and Chambers (2011: 435) postulated, "Once a threshold has been crossed it is often ecologically and economically difficult, if not impossible, to return the system to its original state." Garner et al. (2019) had a similar view, noting that eastern portions of the sagebrush biome that are uninvaded by cheatgrass should be prioritized for protection from future invasion because areas with low resilience and resistance to invasive annual grasses in the Great Basin had already been overtaken.

Karl and Chambers (2019: 145) illustrate a state-and-transition model (Figure 6) in which livestock are a key factor in initiating annual grass invasions, converting sagebrush understories to a heavily-invaded state, which then burns to eliminate the sagebrush overstory and reach a cheatgrass monoculture.

Brooks and Chambers (2011: 433) defined native ecosystem processes and components that contribute to healthy ecosystem function and recovery following disturbance as "ecological memory," and noted that in drier areas of North America, livestock grazing has significantly influenced ecological memory, altering native plant community resistance to non-native invasion.



① Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush like prolonged or severe drought, freezing, flooding, wildfire, insects, disease, and pathogens.

(2a) Sagebrush increases with time until co-dominant with the herbaceous understory.

(2b) Perennial grass, sprouting shrubs, and forbs become dominant due to disturbances that decrease sagebrush.

(3a) Sagebrush increases with time until dominant.

(3b) Perennial grass and forbs increase due to disturbances that decrease sagebrush.

(T4) Continuous spring grazing with cattle during the critical growth period of cool season grasses results in dominance of grazing tolerant species that may include warm season grasses (e.g., blue grama). As bare ground increases, surface erosion (e.g., rills, sheet erosion) and pedestalled plants (especially bunchgrasses) may result.

(R4) Light to moderate grazing with periodic rest during critical growth periods along with fire, herbicides, and/or mechanical treatments can result in return to reference state.

(T5) An increase in the disturbance cycle by fire, fire surrogates, mechanical types of disturbance, and/or high density/frequency grazing will favor sprouting shrubs such as rabbitbrush. Annual invasives can occur.

(6a) Sagebrush increases with time. Cheatgrass and other weeds can be present, but do not dominate.

(6b) Perennial cool season grasses increase due to disturbances that decrease sagebrush. A temporary flush of annual invaders is expected.

(7a) Sagebrush increases with time and removal of disturbances until co-dominant with herbaceous understory.

(7b) Perennial cool season grasses and sprouting shrubs increase due to disturbances that decrease sagebrush.

(T8) Perennial grasses and forbs are eliminated and sagebrush increases with high density/frequency grazing by cattle, resulting in altered biotic, hydrologic, and soil function. This state is at-risk to invasion by annuals such as cheatgrass, especially after a stand-replacing, sagebrush killing event.

(T9) If a cheatgrass seed source is introduced, and weather conditions are conducive to establishment (warm wet spring), it will invade, especially after a stand-replacing event that eliminates sagebrush.

⑩ Fire and fire surrogates that kill sagebrush will dramatically increase cheatgrass.

(T11) Multiple chemical and/or mechanical treatments or biological disturbances that reduce sagebrush will result in a shift toward sprouting shrub dominance with potential for cheatgrass to invade.

(T12) Catastrophic climatic events and/or fire can result in cheatgrass dominance, especially when in the sagebrush dominant phase of the altered state.

(R12) A restoration treatment, including chemical treatment for cheatgrass and seeding can restore a perennial grass community and eventually support an altered sagebrush community with invaders.

(13a) Sagebrush increases with time and no disturbances until co-dominant with the herbaceous understory, but cheatgrass will be present.

(13b) Perennial grass and forbs become dominant due to disturbances that decrease sagebrush.

(14a) Sagebrush increases with time and no disturbances until dominant, but cheatgrass may be present.

(14b) Perennial grass and forbs become dominant due to minor disturbances that decrease sagebrush.

⑮ Perennial grass and annual/perennial forbs become dominant due to disturbances that decrease sagebrush.

Figure 6. State-and-transition model for Wyoming big sagebrush communities, showing high density/frequency grazing by cattle as a key precursor to cheatgrass invasion. Reproduced with permission from Karl and Chambers (2019).

Resilience and Resistance

Ecosystem resilience and resistance measures can be used as an index of vulnerability to cheatgrass invasion and fire (Maestas et al. 2016). Resilience is the ability of ecosystems to restore themselves after disturbances like fire, while resistance is the ability of ecosystems to remain largely unchanged in the face of disturbances or weed invasion (Stringham et al. 2003, Maestas et al. 2016). Roundy et al. (2018) used cheatgrass cover as a surrogate for resistance, with more resistant sites having less cheatgrass cover, while perennial grass cover was a surrogate for resilience, with areas with greater perennial grass cover having greater ability to return to a natural state following disturbance. Ricca and Coates (2020) suggested that soil type, moisture levels, and biota can result in differences in resilience and resistance of plant communities to invasion and conversion to cheatgrass monoculture. Land uses are often at the root of diminished resilience, which can be altered when disturbance patterns depart from historical norms (e.g., inappropriate livestock grazing or clearcut logging)(Brooks et al. 2016b).

Wyoming big sagebrush and salt desert shrub communities have the lowest resilience and resistance (Maestas et al. 2016, Brooks et al. 2016b). Low productivity ecosystems in harsh cold desert environments generally have lower resilience (Chambers et al. 2014). Figure 7, reproduced from Wisdom et al. (2005), shows habitat resiliency and quality in the Columbia Plateau ecoregion as high (Class 1), moderate (Class 2), and low (Class 3). For multiple species of *Bromus*, Brooks et al. (2016b) also rated creosote scrub, blackbrush, subalpine forest, and mountain grasslands as having low resilience under historical disturbance regimes; chaparral, pinyon-juniper, mixed conifer, mountain sagebrush, western plains grasslands, and perennial grassland having high resilience; with fires, overgrazing, and nitrogen deposition reducing resilience.

Resistance is the ability of a plant community to retain its existing processes, functions, and structure in the face of stressors, including disturbance and invasive species, while resilience is the capacity of a community to regain its structure, processes, and functions after it is altered by such stressors (Chambers et al. 2016). Resistance of sagebrush communities to cheatgrass invasion was high in areas that had high levels of native perennial herbaceous species (Chambers et al. 2007). Resistance to *Bromus* spp. generally increases with increasing summer precipitation; areas with predominantly winter precipitation are more susceptible to *Bromus* invasions (Chambers et al. 2016). Areas with cooler soil temperatures and wetter soil moisture regimes are associated with greater resilience and resistance (Roundy et al. 2018). According to Garner et al. (2019), in high-resilience habitats, recovery potential is high until cheatgrass reaches 25% cover, and beyond that recovery potential is at least moderate. In low-resilience habitats, once cheatgrass exceed 5% cover, these researchers rate recovery potential as low.

Ecological Consequences of Cheatgrass Invasion

Bromus tectorum has long been recognized as a source of system impoverishment and altered ecosystem dynamics (Billings 1992). According to D'Antonio and Vitousek (1992), the effects of invasive grasses are significant locally, regionally, and globally, and represent a substantial threat to biological diversity. Invasion of cheatgrass into lower elevation, more xeric sites and alteration of fire frequencies result in reduced plant diversity and habitat structure (Connelly et al. 2004, Crawford et al. 2004). Cheatgrass invasion also corresponded to a decrease in native species at higher elevations in southern Idaho (Bagchi et al. 2013). Knick and Rotenberry (1995) asserted that conversion to cheatgrass monoculture results in an irrevocable loss of wildlife habitat, contributing to shrubsteppe habitat fragmentation.

Under pristine conditions, short-lived perennial grasses and root-spouting shrubs recolonized sagebrush steppe in the wake of fire (Young et al. 1972). Bottlebrush squirreltail (*E. elymoides*) and big squirreltail (*E. multisetus*) are native grasses that colonize disturbed areas (Young et al. 2003). In some areas, short-lived perennials such as squirreltail and Sandberg's bluegrass were the original early successional species in sagebrush steppes (Young et al. 1972, Yensen 1981, Shinneman et al. 2018). In other areas, annual fescues were the primary colonizers

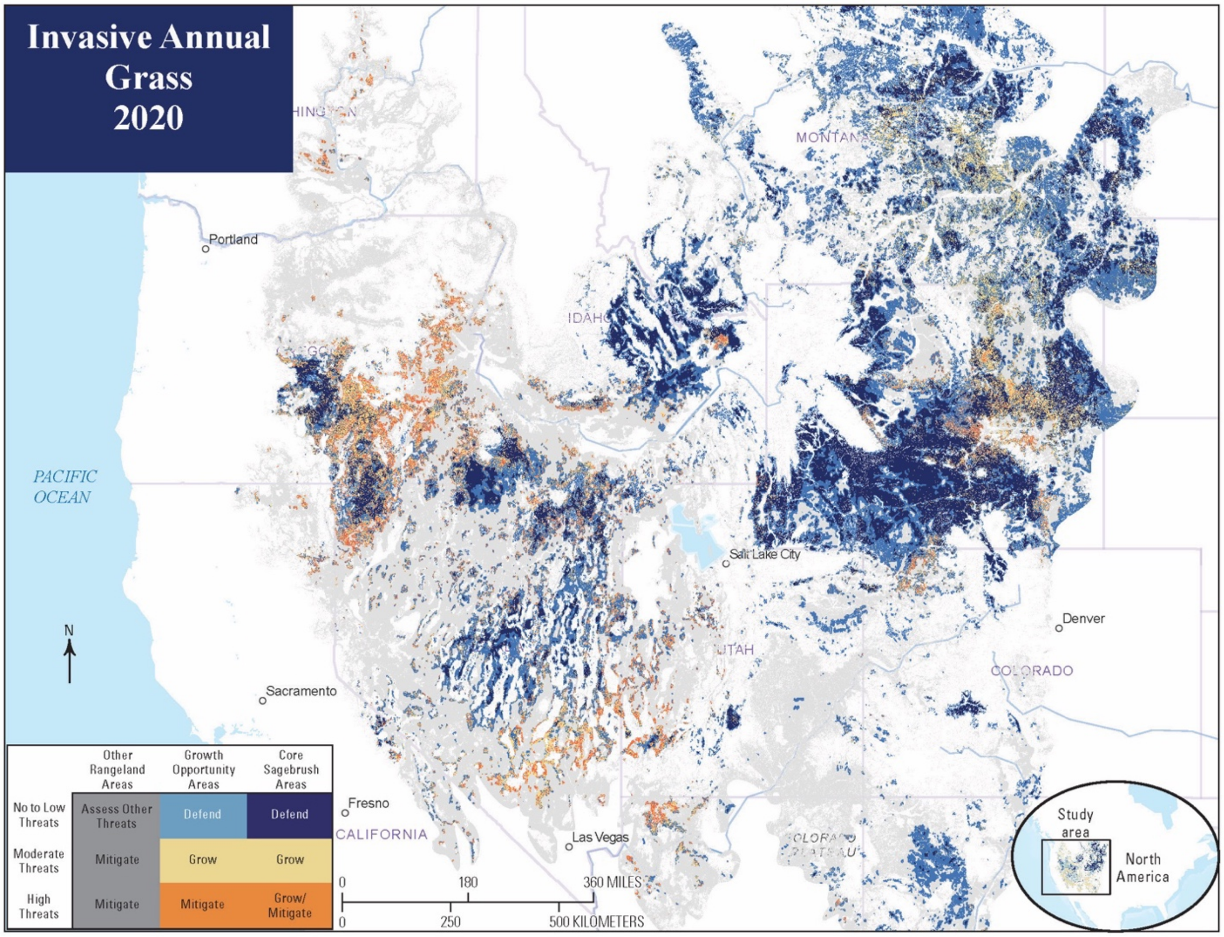


Figure 7. Threat level from invasive annual grasses in sage grouse habitats, reproduced from Doherty et al. (2022).

cheatgrass, and showed significantly greater survival when associated with native bluebunch wheatgrass than with cheatgrass, crested wheatgrass, or burr buttercup (Hall et al. 1999).

Soil changes follow in the wake of cheatgrass invasions. Warmer and drier soils are associated with cheatgrass occurrence and dominance (Roundy et al. 2018). Cheatgrass creates a dense layer of straw-like litter when it dies each year (Evans et al. 2001, Germino et al. 2016). Organic litter delays soil moisture depletion, and holds warmth at night, keeping soil temperatures above critical minima for cheatgrass germination (Evans and Young 1970). Plant litter cover was associated with cheatgrass and non-native forb production on a 1- to 2-year lag (Pilliod et al. 2017). Evans and Young (1970) found a fourfold increase in cheatgrass density on soils with organic litter versus bare ground.

weeds, rather than native species (Germino et al. 2016). Cheatgrass-infested areas can return to Russian thistle and tumblemustard (Piemeisel 1938). Cheatgrass invasion can facilitate medusahead invasion (Eviner et al. 2010).

Results of Cheatgrass-Mediated Fire

Because cheatgrass is an annual that dies in midsummer and becomes tinder-dry, it increases the likelihood and size of fires. Mack (2011) placed the damage that cheatgrass causes after death in forming highly combustible fuel and feeding greater fire frequencies, as dwarfing the damage it causes as a competitor while alive. Fire radically reduces sagebrush and juniper, and these woody species are quite slow to recolonize following fire (West and Yorks 2002). Greater fire frequencies result in lower diversity in native plant communities (Pellant 1994).

Plant and animal species in areas now prone to widespread wildfires are at considerable risk of extirpation, resulting in biological and genetic diversity losses, as well as decreases in ecosystem function (Billings 1994:29). The common sagebrushes do not re-sprout following fire, but rely on seeding from surviving shrubs; Wyoming and basin big sagebrush showed poor seedling recruitment overall following fire (Lesica et al. 2007). Sagebrush does not resprout from stumps following fire, whereas rabbitbrush and horsebrush do (Young and Evans 1978). Whisenant (1990) pointed out that sagebrush can re-establish following fire from seed, but its seeds are relatively short-lived, so if fire returns again within 4-6 years after an initial burn, sagebrush can undergo local extinction. According to Lesica et al. (2007), mountain big sagebrush took an average of 32 years to recover post-fire, basin big sagebrush recovery took 26 years, while Wyoming big sagebrush recovery was extremely slow, with only 2% recovery after 23 years. Billings (1994) found that sagebrush had scarcely returned to a burn site after 45 years. O'Connor et al. (2020) found that post-fire sagebrush seedling recruitment was dependent on soil moisture the March following the fire, and that drought could cause a failure of sagebrush seedings to take root. If fire return intervals are too short, sagebrush is unable to re-establish before the next burn, effectively excluding this shrub from the landscape (Lesica et al. 2007). In salt-desert scrub communities, shadscale and budsage (*Picrothamnus desertorum*) do not resprout following fire, while other shrubs species that do resprout are at least reduced following fire (West 1994).

Fire reduces infiltration of water into the soil, and results in high levels of turbid runoff (Buckhouse 1985). Cheatgrass-dominated sites show about twice the runoff and half the water infiltration of native sagebrush-grassland sites (Germino et al. 2016). According to Mack (2011: 255), "Cheatgrass delivers an environmental *coup de grace* the following autumn, when precipitation resumes. The cheatgrass-dominated landscape, having been denuded by fire, becomes dissected by erosion; the resulting sediment soon finds its way into regional waterways."

Cheatgrass invasion results in habitat fragmentation, both before and after fire. Cheatgrass dominance contributes to shrub patch fragmentation by facilitating the spread of subsequent fires (Knick and Rotenberry 1997). Large, species-poor tracts of cheatgrass monoculture have the effect of isolating remaining pockets of native vegetation (Rosentreter 1994). Shrubsteppe has been fragmented by fires caused by agriculture, military training operations, and natural ignitions (Knick and Rotenberry 1997).

Effects of Cheatgrass on Wildlife

Biological invasions are second only to land-use change as a cause of extinctions worldwide (D'Antonio and Vitousek 1992). Litt and Pearson (2013) reviewed the literature and concluded that cheatgrass invasions are associated with a decreased abundance and occurrence of native rodents, sagebrush. and grassland birds, although ants, burrowing owls, and long-billed curlews may increase. Ostoja et al. (2009) found that ant abundance, particularly for seed-harvesting genera, was tenfold greater in cheatgrass-dominated plots than in intact sagebrush plots, but that rare species of ants were less abundant in cheatgrass-dominated areas. Cheatgrass adversely affects pygmy rabbits and greater sage-grouse, while red brome adversely affects desert tortoises (Germino et al. 2016). A primary reason for this latter finding is that desert tortoise caught aboveground during a fire have little chance to escape incineration (Brooks and Esque 2002). Desert tortoises are very uncommon in annual grasslands (Ibid.). This is because fires eliminate shrubs required by desert tortoises for cover, and also replace native annual plants valuable as tortoise forage with unpalatable invasive grasses (Brooks and Esque 2002). Hall et al. (2009) found a negative relationship between cheatgrass cover and abundance of snakes.

Rodents appear to be particularly harmed by cheatgrass invasions. Larrison and Johnson (1973) found that while degraded sage steppe and salt desert scrub communities retained robust populations of rodents. Meanwhile, rodents were almost entirely absent from cheatgrass monoculture areas. Cheatgrass-dominated areas had reduced numbers of rodent species and a lower abundance of rodents than did sage-steppe areas (Ostoja and Schupp 2009). Small mammal densities were significantly lower in cheatgrass-dominated fire scars (Moritz 1988). Increasing cheatgrass density results in decreases in the diversity and abundance of small mammals, with potential consequences for populations of their predators, from badgers to raptors (Freeman et al. 2014, Germino et al. 2016). Holbrook et al. (2016) documented that cheatgrass has a significant negative effect on ground squirrel abundance, fire in an uninvaded shrubsteppe has a positive effect on ground squirrel populations by eliminating shrubs and stimulating bunchgrass growth, while fire in a cheatgrass-invaded setting imposed an additional negative stressor on ground squirrel populations. However, even though cheatgrass invasion radically increases the abundances of available seeds, populations of granivorous rodents may show no population response (Lucero et al. 2015). Ceradini and Chalfoun (2017) found mixed results in response of rodent assemblages to cheatgrass invasion, with a few species increasing or decreasing, but most remaining largely unchanged in abundance.

The effect of seed predation by birds and rodents on grass establishment can be an important determinant of plant succession. Nelson et al. (1970) found that rodent depredations resulted in 98% loss of broadcast seeds within 6 weeks in plots where poisoned grains were not applied, while birds (particularly chukar partridges) caused 93% loss of broadcast seeds over the winter months on plots protected from rodents (Nelson et al. 1970). In field experiments, granivorous rodents and birds, as well as ants, preferred the seeds of native plants, and avoided cheatgrass seeds (Kelrick et al. 1986, Lucero et al. 2015). Ostoja et al. (2013) found that cheatgrass seeds were least preferred among all seeds by western harvester ants. Seed predation by ants may pose a significant problem for aerial seeding efforts on cheatgrass-dominated sites (Ostoja et al. 2009). Small mammals selected cheatgrass seeds significantly less often than seeds of native species in both forest and steppe environments (Connolly et al. 2014). In the Great Basin, rodent selection for the seeds of native grasses, and avoidance of cheatgrass seeds, resulted in the suppression of seedling establishment for native grasses but not for cheatgrass (Lucero and Callaway 2018a). Thus, the preference of native granivores for the seeds of native grasses can help to accelerate cheatgrass invasions.

The reduction in small mammals as a result of conversion to cheatgrass monoculture has adversely affected populations of golden eagles and prairie falcons in the Snake River Birds of Prey National Conservation Area (Sands et al. 1999). According to Steenhof et al. (2000), prairie falcon numbers in this area have declined significantly over time, particularly in the eastern part of the NCA where fires and agriculture have had the heaviest impact; burrowing owl nesting pair numbers have increased over time. In the same area, populations of jackrabbits have declined significantly as a result of livestock grazing, cheatgrass invasion, and fire, while populations of ground squirrels fluctuate greatly and are less viable as a raptor food source in cheatgrass-dominated areas than in native vegetation (Yensen et al. 1992, Knick et al. 2000). Steenhof et al. (2000) linked the twin declines of jackrabbit and golden eagle populations on the Snake River Birds of Prey National Conservation Area to shrub loss caused by frequent fires.

Like livestock, wild herbivores may forage on cheatgrass for a short period before it sets seed, but otherwise the impacts of cheatgrass on wildlife are uniformly negative (Boyte and Wylie 2016). Rosentreter (1994: 171) observed, "A reduced period of active green vegetation means a reduced period when wildlife and domestic livestock can properly utilize an area." Native herbivores that will use cheatgrass when it is green in spring include elk (Buechner 1952), deer and pronghorn (Mealor et al. 2013), and bighorn sheep (Reid et al. 2008). In western Montana, Kohl et al. (2012) found that elk use of cheatgrass in different populations averaged from 0% to 21.5% of the winter diet and averaged from 4.5% to 13.7% of the spring diet. Herbivores found green forage in uninvaded sagebrush stands for up to a month longer than in adjacent cheatgrass monocultures (Rosentreter 1994). Cheatgrass is not a significant component of pronghorn diet (Johnson 1979). Pronghorn, elk, and mule deer used cheatgrass-dominated fire scars slightly more, but not always significantly so, than control areas (Moritz 1988).

Horses fare better on a diet of cheatgrass than cattle, and unlike cattle they are not prone to mouth sores from the awns (Klemmedson and Smith 1964). Ganskopp and Vavra (1986) found that wild horses exhibited neither preference for, nor avoidance of, cheatgrass-invaded habitats versus native vegetation, when multiple bands of horses were considered. Horses are capable of surviving and maintaining weight on cheatgrass after it has dried (Stewart and Young 1939). Hansen et al. (1977) reported that cheatgrass made up 9% of the diet of wild horses and 7% for cattle, and both selected a similar high proportion of native bunchgrasses; cheatgrass made up 1% of mule deer diet (*and see* Hubbard and Hansen 1976). While King et al. (2019) found that wild horses can transport cheatgrass viable seeds and deposit them in their feces, there is an absence of research demonstrating that wild horses are a significant vector of cheatgrass dispersal.

Once cheatgrass attains dominance, sagebrush-dependent wildlife species decrease or are extirpated, while generalist species of wildlife may be able to persist (Germino et al. 2016). Earnst and Holmes (2012) found that grassland-associated birds were less abundant in shrubsteppe with cheatgrass understory than in shrubsteppe with native bunchgrass understory, while shrub-associated birds were not. Ground-nesting birds experience marginal nesting habitat in sagebrush heavily invaded by cheatgrass, due to the lack of adequate concealment cover; in particular, Brewer's sparrows and sage-grouse largely disappear from annual grasslands (Sands et al. 1999). Accelerated fires due to cheatgrass infestations negatively affect populations of loggerhead shrike (Humple and Holmes 2006). Conversion to cheatgrass has reduced populations of sage-grouse, black-tailed jackrabbits, and golden eagles (Brooks 2008a). Elimination of sagebrush as a result of cheatgrass-fueled fires eliminates requisite habitat for 11 species of sagebrush-obligate birds and mammals (Pyke et al. 2016).

Sage-grouse nest site selection is negatively correlated with cheatgrass (Kirol et al. 2012, Lockyer et al. 2015). Sage-grouse leks surrounded by habitats impacted by exotic grasses showed low male recruitment following heavy precipitation years, while unimpacted leks showed high recruitment of males following high-precipitation years (Blomberg et al. 2012). Sage grouse selected nest sites with greater shrub cover and less cheatgrass; cheatgrass abundance was the single greatest factor influencing nest site selection (Lockyer et al. 2015).

The cumulative loss of sagebrush habitats to cheatgrass invasion and fire has contributed strongly to sage grouse declines at large spatial scales (Coates et al. 2015). Downs et al. (2016) used remote sensing to estimate that 60.3 million acres of land within the historic range of greater and Gunnison sage grouse have at least 2% cover in cheatgrass. Doherty et al. (2022) mapped cheatgrass extent within high-value sage grouse habitats and other rangeland areas, finding 8.1 million acres of high-value (core and growth opportunity area) sage grouse habitats are at high threat level for cheatgrass invasion and 18.8 million acres more are at a moderate threat level, while 35.5 million acres of other rangeland areas are rated high and 19.4 million acres are at moderate threat level (see Figure 7). Brooks et al. (2015) ranked fire as one of the top three threats to sage-grouse rangewide, and a top-two threat in the western half of its range. Greater shrub cover was the greatest single factor contributing to nest survival in one study (Lockyer et al. 2015). Modeling indicates that large fires occurring at high frequencies are likely to cause sage-grouse population extirpations, whereas small fires at low frequencies benefit sage-grouse in the absence of domestic sheep grazing (Pedersen et al. 2003). Fire has long-term adverse effects on sage grouse population growth rates, and approximately half of the present sage grouse population will be lost in the Great Basin if current fire trends continue (Coates et al. 2015). Conversion of sagebrush to exotic grassland lowered adult survival and had a negative impact on sage grouse populations (Blomberg et al. 2012). Fire scars dominated by cheatgrass were used significantly less by sage grouse (Moritz 1988). Foster et al. (2019) found that sage grouse returned to burned areas to nest, rather than moving to unburned habitats, but suffered lower nest success and lower adult survival in burned habitats. Sage grouse experienced depressed nest success rates 10 years post-fire (Lockyer et al. (2015). Given the strong linkage of cheatgrass to fire on degraded rangelands, fire can be considered a major indirect impact of cheatgrass on sage-grouse.

Cheatgrass as a Livestock Forage

Invasive weeds can reduce forage productivity for livestock (Eviner et al. 2010). However, where it is present, cheatgrass can be a common component of the diets of cattle and domestic sheep (Hubbard and Hansen 1976, Johnson 1979). During years with adequate moisture, cheatgrass forage yields are similar to those of perennial grasslands (Klemmedson and Smith 1964, Harris 1967), and at certain brief times of year cheatgrass has high nutrient and preference value for both sheep and cattle (Harris 1967). It is considered fair to good forage for livestock when green in the spring, but forage quality decreases significantly after the inflorescence emerges (Mealor et al. 2013). The live portion of the cheatgrass life cycle, from green-up to seed set, lasts only 6 to 8 weeks (DeFlon 1986). Because cheatgrass completes its lifecycle and dies in early summer, cheatgrass-dominated plant communities are far less productive because they are not sustaining plant growth through the summer growing season (Pellant 1996). By fall, cheatgrass is deficient in protein, and feeding of livestock with nutritional supplements is required (Schmelzer et al. 2014).

In some regions of the West, cheatgrass is the most important forage plant for livestock (Klemmedson and Smith 1964). In areas that have attained monoculture status, there is very little else for an herbivore to eat. Cheatgrass can be used for livestock forage during spring grazing, and has even been suggested as a winter and spring forage for livestock on public rangelands (Pellant 1996 and Upadhyaya et al. 1986). Cheatgrass ranges may provide the bulk of spring grazing for cattle and are important spring lambing range (Stewart and Hull 1949, Hironaka 1961, Murray and Klemmedson 1968, Pellant 1996).

On heavily invaded lands, cheatgrass contributes more feed for livestock than any other plant during spring, but forage production fluctuates greatly from year to year based on precipitation (Cook and Harris 1952). Since this forage production fluctuates, it is difficult for livestock operations to plan for a given year. Cheatgrass produced significant forage on lands that had been producing Russian thistle and tumblemustard, and therefore cheatgrass was initially hailed by many involved with the range livestock industry as "the greatest thing that could have happened to sagebrush rangelands" (Young and Allen 1997: 532). DeFlon (1986) extolled greasewood or shadscale with a cheatgrass understory as the ideal winter range for cattle, noting, however, that protein supplement was required. Johnson (1979) found that cheatgrass made up 26% of cattle diets and 23% of domestic sheep diets on portions of the Idaho National Laboratory open to livestock grazing. Ranching operations might take advantage of cheatgrass for spring forage, but native forage provides superior grazing by early summer (Maher 2007). While the majority of Wyoming and Colorado ranchers believe that cheatgrass is a problem, some still rely heavily on cheatgrass for early spring grazing (Kelley 2010). Cook and Harris (1952) even suggested that low-productivity soils should remain in cheatgrass as spring range for livestock, instead of being converted to native bunchgrasses. Cheatgrass was purposefully planted by the U.S. Department of Agriculture in an effort to identify a more resistant forage species for degraded rangelands (Mealor et al. 2013).

Cheatgrass is unpalatable to livestock and therefore of limited forage value due to its sharp awns, sparse leaves, tough stems, and the short period when it is green (Pickford 1932, Stewart and Young 1939). There is broad agreement that cheatgrass that has dried is an unpalatable forage and its dry, sharp awns can cut the mouths and injure the eyes of cattle and sheep (Upadhyaya et al 1986, Knapp 1996, Young and Allen 1997, Kaczmarski 2000, Mealor et al. 2013). These injuries commonly result in secondary infections (Young and Allen 1997). Cheatgrass seeds can puncture either the eyes, causing blindness, or the mouth and throat of livestock, causing lumpy jaw (Knapp 1996, Young et al. 1987). In addition to puncturing the mouth and skin, awns can puncture intestines of livestock, causing discomfort and reduction of feed intake (Upadhyaya et al 1986). That said, cheatgrass seeds dehisce so rapidly at maturity that the period of potential injury is transitory (Young and Clements 2007: 17).

Cheatgrass has lower palatability than perennial grasses, but livestock will graze it readily, particularly in spring when it is green (Warg 1938, Stewart and Hull 1949 Klemmedson and Smith 1964, Young and Allen 1997). Cheatgrass harvested in mid-June after drying has about half the protein and significantly less key minerals than native grass species (Murray et al. 1978). Digestible protein in cheatgrass was deficient after mid-May (Cook and Harris 1952). Once native perennials are mature, they also provide a protein-deficient forage for livestock, but shrubs form an important protein supplement for livestock in late summer and fall, and these are largely absent from areas that burn and are replaced by cheatgrass (Young and Clements 2007). According to Stewart and Hull (1949), dry cheatgrass is grazed by cattle but not sheep, and the cattle will lose weight grazing on it without supplementation of their diets. Animals grazing on dry cheatgrass show a deficiency in vitamin A within 90 to 120 days, but in less time suffer from internal disorders causing abortion unless the diet is supplemented with alfalfa, hay, or shrubs (Cook and Harris 1952).

Cheatgrass can provide abundant forage during wet years, but during dry years produces almost no forage, and this variability from year to year in forage production makes cheatgrass a poor basis for long-term livestock operations (Young and Allen 1997). Perennial grasses produce roughly double the forage of cheatgrass on a per-acre basis during years of abundant precipitation, and during dry years the forage production advantage of perennial grasses can be more than 12 times as great (Stewart and Young 1939). Modeled production of cheatgrass varied tenfold from year to year, making cheatgrass an unreliable source of forage (Mata-González et al. 2007). Cheatgrass production is virtually nil during drought conditions (Young and Allen 1997).

In saltbush communities, shrubs provide an important protein source for livestock (Young et al. 1987). Thus, when fires convert heavily-invaded salt desert shrublands to cheatgrass monoculture, this protein supplement is eliminated. Maher (2007) found that cheatgrass invasion increases the likelihood of ranch bankruptcy because cheatgrass-related fires result in closure of burned federal lands to livestock grazing for at least two years. The invasion status of cheatgrass itself, in the absence of fire, appeared to have no significant effect on ranch bankruptcies. Ranchers often view cheatgrass as a slight to moderate problem, whereas the vast majority of land managers view cheatgrass as a moderate to extreme problem (Kelley 2010).

Expected Cheatgrass Trends under Climate Change

Climate change is expected to have a major impact on weather patterns in the Great Basin in the coming century (Chambers 2008) and is projected to shift the spatial distribution of entire biomes across the American West (Rehfeldt et al. 2012). With a changing climate, atmospheric carbon will reach levels triple pre-Industrial thresholds, mean annual temperatures will be hotter, drought stress will increase, and soil moisture levels will be lower (Bradley et al. 2016, *sensu* Dukes and Mooney 1999, Seager et al. 2007). Ford et al. (2012: 80) projected that "[d]isturbances such as fire, drought, grazing, urbanization, and energy development are predicted to have a heightened impact on the western United States under a changing climate."

Climate models forecast multiple outcomes over the coming decades. Ford et al. (2012) predicted decreased annual precipitation in the Southwest and Central Rockies regions. Palmquist et al. (2016) modeled climate change for the sagebrush biome, and projected increasing temperatures, increasing winter and spring precipitation, but longer, drier summers, changes expected to increase cheatgrass spread. Reduced summer precipitation is predicted by most climate change models, and this outcome would result in the expansion of areas potentially invaded by cheatgrass (Bradley 2009). A predicted increase in winter rain instead of snow as a result of climate change is predicted to increase cheatgrass spread on the shortgrass prairies along the base of the Colorado Rocky Mountains (Prevéy and Seastedt 2015). Earlier spring snowmelt due to a changing climate has already led to longer fire seasons (Westerling et al. 2006). Finch et al. (2012) hypothesized that while sagebrush is relatively frost-tolerant, warming temperatures could allow frost-intolerant shrubs to outcompete and displace sagebrush. Friggens et al. (2012) stated that by 2100, 55% of future landscapes in the American West are likely to have climates incompatible with the vegetation types of the present day.

Climate change is likely to exacerbate cheatgrass spread

Bradley et al. (2016) predicted that climate change would increase the spread of both red brome and cheatgrass. Cheatgrass range is likely to contract in the southern part of the Great Basin, while a major range expansion could occur northward in Wyoming and eastern Montana (Bradley and Wilcove 2009, Mack 2011, Friggens et al. 2012). With climate change, red brome may be able to expand in portions of the southern Great Basin no longer suitable for cheatgrass due to increasing aridity (Bradley et al. 2016). In addition to the southern Great Basin, red brome may decline on the Colorado Plateau as cheatgrass shifts northward (Bradley et al. 2016).

Some other models predict a smaller area of cheatgrass dominance with a changing climate. Land area suitable for cheatgrass invasion could expand by a further 45% or decrease by as much as 70%, depending primarily on precipitation conditions (Bradley 2009). However, most climate change scenarios result in a constriction of the suitable range for cheatgrass (Bradley 2009). Brooks and Pyke (2002) predicted that with drier-than-normal conditions in the western US over the succeeding 25-35 years, many invasive species of plants would be likely to decline in dominance. But Bradley et al. (2010) caution that climate change involves multiple variables including nutrient availability, precipitation patterns, and temperature changes that could affect the spread or contraction of invasive species like cheatgrass, and therefore predicting the magnitude and locations of cheatgrass spread in the future is difficult.

Cheatgrass is likely to expand into higher elevations if temperatures rise and ground disturbances continue (Williamson et al. 2019). Warming temperatures increase cheatgrass population growth directly, increasing both survival and fecundity, with the largest increases occurring during the wettest years. Higher temperatures increase vegetative biomass but decrease seed production (Wade 2015). Blumenthal et al. (2016) demonstrated that warmer temperatures more than tripled cheatgrass biomass and seed production in a High Plains study site, enhancing its ability to grow when native plants were dormant, but that boosting carbon dioxide concentrations had no effect. However, Larson et al. (2017) did not find an increase in cheatgrass with warming temperatures or drier conditions, nor did fire change this calculus. Warming temperatures increase cheatgrass population growth indirectly because cheatgrass survival is hindered by snow cover (Compagnoni 2013). With warming temperatures, snowfall will in some cases be replaced by rain, increasing the ability of cheatgrass to spread (Abatzoglou and Kolden 2011, Concilio et al. 2013). However, timing of precipitation remains key. Bradley (2009) projected that increases in summer precipitation could make native grasses and shrubs more competitive with cheatgrass because they could take advantage of summer rainfall after cheatgrass had already senesced.

Increasing CO_2 concentration in the atmosphere can favor invasive species of plants (Pendleton et al. 2013) and is likely to exacerbate cheatgrass invasions in particular (Nowak et al. 2004). Rising CO_2 levels are likely to give annual grasses a competitive advantage in ecosystems with depleted herbaceous species or low resistance to invasion, but this competitive advantage may not occur in plant communities with relatively high resilience and resistance (Chambers et al. 2014). Smith et al. (1987) reported that cheatgrass had the most consistently positive response to high atmospheric carbon dioxide concentration, and postulated that elevated atmospheric CO_2 levels are likely to result in further competitive advantage for cheatgrass over native grasses, facilitating its spread. At a Mojave Desert site, Smith et al. (2000) found that increasing atmospheric carbon dioxide resulted in greater cheatgrass biomass and seed production, and ultimately a greater overall proportion of cheatgrass among all plants. Ziska et al. (2005) found that cheatgrass increases in productivity with increasing atmospheric carbon dioxide, but also decreases in digestibility and forage value due to increasing lignin and cellulose. Salo (2005) suggested that increasing atmospheric carbon paired with nitrogen deposition has facilitated recent red brome expansion. Increased atmospheric CO_2 also increases growth and water-use efficiency in native grasses, and thus greater success in revegetating degraded ranges is possible when cheatgrass can be removed or suppressed (Smith et al. 1987).

Fossil fuel combustion and fertilizer applications are increasing the amount of available nitrogen, potentially favoring invasive plant species (Bradley et al. 2010). Pendleton et al. (2013) asserted that invasive annual grasses are particularly responsive to nitrogen deposition, downwind from pollution sources. Increasing nitrogen deposition could give cheatgrass a further advantage over native plants (Chambers et al. 2014). In response to nitrogen deposition, cheatgrass increased its growth and competitive ability, while native grasses did not (He et al. 2011). Coastal sage scrub is readily converted to cheatgrass after several fire cycles, and nitrogen deposition can accelerate this process (Fenn et al. 2003). By contrast, Concilio and Loik (2013) found no effect of increased nitrogen deposition on cheatgrass cover and dominance at high elevations. Atmospheric nitrogen deposition is quite voluminous from pollution plumes downwind of major metropolitan areas, coal-fired power plants, or large agricultural operations, although most of the arid West is characterized by low levels of atmospheric nitrogen deposition (Fenn et al. 2003).

Areas currently considered too high in elevation to support serious cheatgrass infestations could become vulnerable because of the changing climate. According to Abatzoglou and Kolden (2011), reduced snowpack and a shift in precipitation from snow to rain may also promote *B. tectorum* invasions and expansion at higher elevations where it is currently limited by short growing seasons. Cheatgrass is expanding in high elevation shrubsteppe in Wyoming, a trend expected to accelerate as longer, drier growing seasons suppress native perennial grasses (Mealor et al. 2012). Mean cover of cheatgrass at a high-elevation site in Rocky Mountain National Park increased more than fivefold between 1993 to 2007 (Bromberg et al. 2011). West et al. (2015) estimated that area habitable by cheatgrass would expand from a current 5.5% of Rocky Mountain National Park to 20.4% by 2050, chiefly as a result of climate change. West et al. (2015) predicted that cheatgrass would be found at altitudes up to 10,800 feet by 2050 due to climate change.

Fire regimes have changed across the western United States, and particularly in sagebrush ecosystems, with longer fire seasons, more acres burned, and shorter fire-return intervals (Shinneman et al. 2018). The Intermountain West is predicted to experience lower relative humidity over the next century, increasing the number of days of high fire danger (Brown et al. 2004). Future climate modeling indicates that fire weather and fuel loading could lead to more widespread fires in coming years (Shinneman et al. 2018). These favor continued cheatgrass expansion. Yue et al. (2013) modeled acreage burned based on multiple climate models for the mid-21st Century and predicted an increase in acres burned in multiple ecoregions, although their model was less predictive for some of the ecoregions where cheatgrass invasion is most problematic. Creutzberg et al. (2016) predicted immediate increases in fire severity and cheatgrass spread due to climate changes in eastern Oregon but predicted lower levels of cheatgrass later in the century with respect to projections under the current climate. Abatzoglou and Kolden (2011: 476) forecast that increased annual grass cover and abundance will lead to more extensive and severe wildfires, proliferating the cycle of cheatgrass invasion.

Factors that would tend to favor cheatgrass including increasing atmospheric carbon dioxide, increasing nitrogen deposition, and increasing temperature only go into effect if adequate precipitation is available to support cheatgrass establishment (Bradley et al. 2016). Wet winters in heavily invaded lower elevations, as predicted for the northern Great Basin under climate modeling, is likely to intensify the cheatgrass-fire cycle (Bradley et al. 2016). Possible shifts in precipitation because of climate change are difficult to predict, introducing uncertainty into projections of future cheatgrass expansion (Bradley et al. 2016). But as native species dwindle as their native habitats shift to a hostile climate, cheatgrass will have an opportunity to expand its footprint across the West.

Cheatgrass spread accelerates climate change

The conversion of native sagebrush steppe to cheatgrass monoculture is likely to exacerbate climate change, contributing to further warming, by reducing carbon storage in affected areas. Most temperate grasslands are considered carbon sinks (Jones and Donnelly 2004). So are shrub-dominated deserts. Cheatgrass monocultures exhibit net carbon losses to the atmosphere due to rapid decomposition of root matter (Verburg et al. 2004). Kauffman et a. (2022) documented that conversion from Wyoming big sagebrush communities to cheatgrass reduces carbon sequestration, resulting in an 88 percent decline in aboveground carbon stocks (conversion to crested wheatgrass is also climactically harmful, resulting in an 82 percent decline). The rapid growth and then death of cheatgrass, combined with its shallow root depth, results in incomplete use of soil moisture, reduced carbon sequestration, and accelerated nutrient cycling (Germino et al. 2016). Greater soil porosity beneath cheatgrass accelerates decomposition of soil organic matter (Norton et al. 2004). As cheatgrass invasion progresses, soil carbon decreases in horizons deeper than 60 cm (Rau et al. 2011). According to Meyer (2011: 4), cheatgrass invasion will likely result in much of the Great Basin and surrounding areas becoming net carbon sources.

Cheatgrass-mediated fire accelerates carbon dioxide emissions into the atmosphere (Boyte and Wylie 2016). At a pre-industrial atmospheric CO_2 concentration of 270 μmol/mol, cheatgrass burned with significantly less heat released than plants subjected to higher atmospheric CO_2 concentrations; modern fires burn hotter than in pre-industrial times (Blank et al. 2006). However, increasing cheatgrass aboveground biomass, as well as decreasing digestibility (and therefore decomposition) both result in greater fuel loads with increasing atmospheric carbon dioxide concentration (Ziska et al. 2005). Cold desert shrublands must be kept intact and protected from burning, if maximizing carbon sequestration is the goal (Meyer 2011).

Zhu et al. (2012) found that the cold desert had about half the carbon stock per square meter as did surrounding coniferous forests. In deserts, more than 95% of organic carbon is stored in the soil (Meyer 2012). Conversion from native bunchgrasses to annual grasses results in a loss of soil carbon storage of 17.8 tons/acre (40Mg/ha) (Koteen et al. 2011). According to Austreng (2012: 21), above-ground biomass increased in the order where: cheatgrass < bunchgrass < sagebrush, corresponding to 1.7, 2.9, and 8.4 $Mg \cdot ha^{-1}$, respectively. According to Meyer (2012: 22),

> "Because cold deserts store much of their carbon belowground and that carbon is stored in deeper soil layers, these deserts are likely to store more carbon per unit area than warm deserts with monsoonal moisture regimes. In addition, the desert shrublands of the interior West might be more appropriately classified as semideserts, as they generally have much higher standing biomass than the true deserts, for example, the Sahara Desert of North Africa, which is virtually plantless over large areas except in drainages ("wadis"). This combination of high belowground allocation and relatively high biomass production appears to make cold deserts exceptionally good candidates for carbon sequestration."

Hooker et al. (2008) found that sagebrush-dominated sites have greater carbon storage in plant biomass compared to crested wheatgrass and cheatgrass systems, due primarily to woody biomass accumulation, paired with greater carbon losses from cheatgrass and crested wheatgrass systems. Conversion from salt desert scrub to cheatgrass results in an eightfold decrease in carbon storage, while conversion from sagebrush steppe to annual grasslands results in a six- to more than fifty-fold decrease in carbon stocks (Meyer 2011). Rau et al. (2011) projected a loss of 6 to 9 Mg/ha of belowground organic carbon with the replacement of perennial bunchgrasses with cheatgrass, without accounting for the loss of sagebrush due to fire. Carbon storage in cheatgrass-invaded areas is much less than native shrublands, and the invasion of cheatgrass has already changed parts of the western US from a carbon sink to a carbon source (Bradley et al. 2006).

Rangelands cover 30% of the Earth's ice-free surface and hold an equivalent amount of the world's carbon (Booker et al. 2013). Grassland carbon storage is more resilient to fire and drought, as opposed to coniferous forests, which are more likely to become carbon sources under these conditions (Dass et al. 2018). Virtually all the carbon in grasslands is in the soil (Jones and Donnelly 2004), and the deep roots of native perennial bunchgrasses promote belowground carbon storage (Koteen et al. 2011). In addition, arbuscular-mycorrhizal fungi are important to soil carbon sequestration, and replacement of native plants with invasive weeds can cause major reductions in VAM and therefore soil carbon (Waller et al. 2020). Replacement of sagebrush by cheatgrass following fire has resulted in a 50% loss in belowground carbon (56 Mg/acre to 29 Mg/acre of carbon) versus sagebrush grassland over a 27-year period (Austreng 2012). The result of conversion to annual grasslands is rapid carbon cycling, much less carbon in deeper soils, and faster carbon cycling leading to shorter fire intervals (Meyer 2012). Austreng (2012) estimated total loss of soil carbon to date as a result of cheatgrass invasion at 60 megatons of carbon and projected that this loss ultimately could exceed 2 gigatons of carbon.

Sagebrush steppe is a net sink of almost twice as much carbon per square meter than cheatgrass-dominated sites, and in late summer, when cheatgrass is dead, cheatgrass-dominated sites are a net carbon source (Germino et al. 2016). Cheatgrass invasion can result in accumulation of organic carbon in the top 20 cm of the soil, but these gains are more than offset by organic carbon losses deeper in the soil (Rau et al. 2011). Larger root diameter and greater lignin and carbon content of sagebrush roots may be driving increased carbon inputs in sagebrush grasslands (Austreng 2012). Soil organic carbon losses are nearly twice the amount of organic carbon as the surface carbon losses from converting perennial bunchgrass to cheatgrass (Rau et al. 2011). This is due to root production and turnover in deep-rooted perennial grasses.

Restoration of cheatgrass-dominated lands to native vegetation offers a key opportunity to help reverse the damage caused by carbon pollution. Restoration of cheatgrass monoculture to sagebrush on all 10 million hectares of cheatgrass-infested land in the Great Basin could compensate for 23% of US annual carbon emissions (Austreng et al. 2011). In addition, increased carbon sequestration also benefits ecosystem health through increased soil water holding capacity, better soil structure, improved soil quality and nutrient cycling, and reduced erosion (Derner and Schuman 2007, Hilty et al. 2004, Rosentreter et al. 2001).

Potential Solutions for Cheatgrass Infestations

Despite decades of effort and a vast body of scientific research, solutions for restoring cheatgrass to healthy native ecosystems remain elusive. Cheatgrass monocultures are considered stable and are difficult to remove (Mealor et al. 2013). Warg (1938: 34) warned, "Because of its widespread infestation, apparent tolerance to range malpractices, high degree of seed viability and growth habits, it is doubtful if eradication or control of *Bromus tectorum* can be accomplished on any large area." Nearly six decades later, Pellant et al. (1996) echoes the early warning, pointing out that the scarcity of workable solutions puts a premium on proper management of livestock grazing to ensure that cheatgrass does not increase. Mack (2011) observed that cheatgrass populations often survive adverse events yet remain dominant. According to Monsen (1994: 45), restoration of sites overtaken by cheatgrass basically requires a full site renovation. Once cheatgrass dominates a site not even cessation of grazing or prescribed grazing treatments have a realistic chance to restore the site to the original flora, according to Vallentine and Stevens (1994). Sanders (1994: 412) advised, "failure is more the rule than success in converting cheatgrass rangelands in southern Idaho to perennial grasses," and further cautioned, "Do not expect the conversion to occur in just a few years."

Anderson and Inouye (2001: 553) counseled that maintaining and recovering native species should be a high priority in the context of warding off cheatgrass. According to Chambers et al. (2007: 142), while it may not always be possible to eliminate *B. tectorum*, it may be possible to limit its abundance. Brooks and Chambers (2011) recommended focusing preventative efforts on uninvaded areas of low resilience and resistance, areas of high conservation value, and areas where invasion is in the early stages and has not yet crossed ecological thresholds. Restoration may be possible in areas with moderate to high resilience, but in invaded areas of low resilience restoration may not be economically feasible once cheatgrass attains dominance (Garner et al. 2019). Areas already dominated by cheatgrass are of low priority for restoration, having already crossed ecological thresholds, argued Brooks and Chambers (2011). Stringham et al. (2003) recommended that once a threshold has been crossed, restoration should focus on repairing damaged ecological processes, not reestablishing a specific plant community. However, according to Chambers et al. (2007), sustainability of western ecosystems depends on maintaining or restoring perennial grasses and forbs.

Mack (2011: 260, internal citations omitted) summarized efforts to control cheatgrass invasions as follows: "In the past 50 years scores of techniques and tools in innumerable combinations have been used in attempting to control cheatgrass in the arid West; singly or in combination, these approaches have failed, often dismally. Detailing these control practices here serves little purpose. To varying degrees, these methods involve alteration (and, often, total destruction) of whatever remained of the native steppe by burning the cheatgrass - infested vegetation, chaining (i.e. mechanically toppling) the sagebrush (*Artemisia* spp.), ploughing, applying herbicides (Monsen et al. 2004a) and then sowing non-native species (e.g. *Agropyron cristatum*, *Agropyron desertorum*, *Kochia prostrata*) on these devastated sites." According to Hulbert (1955: 210), there is no method that will assure complete kill or absence of cheatgrass seeds.

Restoring sagebrush post-disturbance is ecologically important but is difficult and expensive to achieve (Davies et al. 2011a). Reducing stocking rates and artificial seeding were used early on to combat the spread of cheatgrass, but both were costly (Harris 1967). Davies et al. (2011a) contended that there are no cost-effective techniques to control large areas invaded by annual grass. The ineffectiveness of restoration of cheatgrass sites was echoed by Mack (2011: 260) who said that most efforts were counterproductive and even benefited cheatgrass. He observed, "Loss of the essential thin biological soil crust is particularly egregious in this deliberate conversion of badly damaged native communities to communities with other non-native species and low species richness."

Concilio (2013) tested three non-chemical approaches (hand-pulling, solarization with clear plastic sheeting, and sheet mulching with wood chips) to the eradication of cheatgrass in patchy distributions at high elevations in the Sierra Nevada Mountains. Hand-pulling reduced cheatgrass cover and the dominance of cheatgrass in the seedbank, while both soil solarization and sheet mulching were also 99% effective at reducing cheatgrass, but also killed native plants, and re-seeding with native plants was unsuccessful. Because of the persistence of cheatgrass seeds in the seedbank, solarization eliminated all plants but resulted in 100% dominance of cheatgrass in the seedbank. None of these methods were found to be practical over large areas.

Anacker et al. (2010) postulated that there is a window of opportunity early in a plant invasion where eradication is both possible and economically feasible. Carpenter and Murray (2004: 4) proposed an integrated approach combining chemical control, physical control, vegetative suppression, and proper livestock management to keep the cheatgrass constantly under stress, reducing its ability to flourish and spread. Cheatgrass infestations may require multi-year, consistent treatments to eliminate (Garner et al. 2019). Epanchin-Neill (2009) argued that the high cost of post-fire restoration can be justified by the savings in future fire costs that would occur when cheatgrass expansion results. Treatments that reduce cheatgrass in the short term tend to increase native grasses, by making more water and soil nutrients available (Monaco et al. 2017).

Efforts to restore cheatgrass-invaded lands face political obstacles. The fact that many invasive plants are not formally listed as noxious weeds, a requirement for many local and state programs, means that remedial action against many invasive plants face funding and bureaucratic challenges (Mayer 2018). Weed-free hay regulations could prevent distribution of cheatgrass through contaminated hay, but cheatgrass is not considered a prohibited weed under weed-free forage programs in either Colorado or Wyoming (Mealor et al. 2013). As invasive weeds spread on public lands, federal funding appropriated for invasive weed control barely covers base salaries, with little funding to grow the program (Mayer 2018). Long term, programmatic invasive planning by land management agencies is impaired by inconsistent and inadequate annual funding (Mayer 2018).

Some researchers even advocate giving up once cheatgrass monocultures become widespread. Young and Evans (1978) seem to advocate giving up on the restoration of heavily cheatgrass-invaded rangelands, and instead managing them as annual grasslands for livestock production. Mathematical modeling by Moody and Mack (1988) suggests that attacking small satellite populations before they are well-established may be a more effective strategy for invasive weed control than attacking a large, well-established population. Great Basin shrubsteppes have not and may never return to their pre-grazing condition (Condon and Pyke 2018). And some caution that the cure could be worse than the disease. According to Piemeisel (1938: 41), treatments involving excessive grazing or burning could be followed by wind erosion, which is more harmful than cheatgrass invasion.

According to Pyke et al. (2016: 308), replacing cheatgrass and the accompanying fire cycle requires restoration of fire tolerant, competitive perennial grasses and forbs that can exclude cheatgrass once established. Native perennial grasses take 2 to 4 years to recover following drought, and longer if grazed by livestock, whereas cheatgrass bounce back the following year (Stewart and Hull 1949). According to HilleRisLambers et al. (2010: 1155), eliminating human-caused factors that promote cheatgrass is a promising approach for long term restoration efforts. Restoration of sagebrush steppe will be primarily dependent on managing for long periods of stability; habitats subjected to frequent disturbance (road construction, oil and gas development, urbanization, and heavy livestock grazing) favor a completely different assemblage of plants adapted to post-disturbance growth (Quire 2013). Herbicides and/or burning are sometimes used for site preparation in conjunction with restoration efforts (Stromberg et al. 2007). Federal agencies have been criticized for treating cheatgrass-invaded acres but doing little or nothing to halt the existing land uses that led to weed infestations (Donahue 2007). In post-disturbance recovery, removal of disturbance agents like livestock grazing should be prioritized over additional intervention through chemical and mechanical treatments.

From an ecological standpoint, it is essential to reduce cheatgrass to a minor component on the landscape as a means of bringing fire risk back into the historical range of variability, and to restore native species that support native species of wildlife. Complete elimination of annual grasses is unlikely (HilleRisLambers et al. 2010). Monaco et al. (2017) found that herbicide use followed by revegetation decreased cheatgrass cover over the long term, while woody plant removal and burning increased cheatgrass over the long term. While total eradication of cheatgrass may be unrealistic, certain control measures can reduce cheatgrass while increasing native perennial grasses (Monaco et al. 2017). Below is an evaluation of various techniques attempted in the name of cheatgrass eradication, which vary from meeting with modest success, to no success, to a mere distraction from reality, to further exacerbating cheatgrass spread.

Seeding with Native or Non-Native Grasses

Seeding with competing grasses – either native or non-native species – has often been attempted as a means of preventing or combating cheatgrass infestations, with mixed results. Reseeding has been attempted as post-disturbance or post-fire restoration, and also (with less success) in the context of seeding native grasses on lands already dominated by cheatgrass. Seeding with crested wheatgrass (*Agropyron cristatum*) has become increasingly controversial, as this Eurasian grass displays many of the same invasive traits and ecological impacts as cheatgrass.

Re-seeding (paired with rest from grazing) has shown some success in cheatgrass reduction but introduced grasses have not consistently outperformed native grass species. In Oregon salt desert rangelands, native grasses rested from grazing for 25 years produced 2.5 times the plant cover as rangeland that was disked and seeded with crested wheatgrass and Russian ryegrass that was protected from livestock for the same period, but the non-native seedings produced a greater biomass of forage for livestock (Kindschy 1988). Seed mixes dominated by introduced grasses showed lower biomass of cheatgrass when applied than did native seed mixes (Bowles 2011). Ott et al. (2019) found that seeded perennial grasses increased for both native seedings and non-native seedings 16 years post-treatment in areas grazed by livestock, but that non-native grasses slightly outperformed native grasses. Burning and heavy spring grazing are commonly attempted to control cheatgrass, but only small-scale seedings of other grass species have met with any semblance of success (Warg 1938).

Johnston (2011) observed that re-establishing desirable vegetation is critical in controlling cheatgrass, but such vegetation is unlikely to mature quickly enough to prevent cheatgrass plants from compromising reclamation. Post-fire seeding with native and non-native grasses and forbs in burned sagebrush habitats — to suppress cheatgrass and increase forage for livestock — has had little success because seedling establishment has been poor, and because cheatgrass growth in both seeded and unseeded areas has been strong (Beyers 2004). The seeding of intact cheatgrass stands with crested wheatgrass has largely failed (Stewart and Hull 1949). Crested wheatgrass seedings can fail due to unfavorable precipitation patterns and competition with cheatgrass (e.g., Pellant et al. 1999). In southeast Idaho, Ratzlaff and Anderson (1995) found that post-fire seeding with three exotic wheatgrasses and two exotic forbs during drought conditions failed, resulting in less plant cover and greater soil erosion than unseeded areas, which recovered to native plant species.

Seeding can reduce the spread of cheatgrass (Monsen 1994). Mazzola (2008) found that seeding with native grasses increased seedling

A crested wheatgrass planting in southcentral Idaho. Matt Lavin photo courtesy Flickr Creative Commons.

emergence and survival even without nitrogen immobilization treatment; perennials have the potential to establish and form viable populations in invaded areas. Improved seeding techniques can enhance the successful germination of desired plant species (Madsen et al. 2016). Adult squirreltail bunchgrass at cover of 15-20% suppressed cheatgrass seedling recruitment (Booth et al. 2003). The life history stage or stages most limiting to seeded perennial grass establishment remain unknown (Davies et al. 2011a). Ultimately, seeding with native perennial grasses best promotes the recovery of native plant communities (Munson and Lauenroth 2011). In southwestern Idaho, native and exotic perennial grass seedings that appeared to fail at year two were rested from grazing for 7 more years and then the perennial grasses matured and dominated the site (Hilty et al. 2004).

In certain cases, post-fire seeding may be unnecessary. On north-facing slopes, perennial grasses and forbs recovered to pre-fire densities in the absence of supplemental seeding (Kulpa et al. 2012). Brooks and Chambers (2011: 436) posited that many areas where post-fire seedings successfully establish are on high productivity sites, are naturally more resilient to fire, and therefore do not require active restoration in the first place.

Non-Native Seedings

To date, post-fire seeding has primarily consisted of non-native perennial grasses such as crested and Siberian wheatgrass, and non-native forbs including alfalfa and forage kochia (Eiswerth et al. 2009). Crested wheatgrass seedings in burns to discourage cheatgrass were commonplace from the 1950s to the 1970s (Pellant 1996). Crested wheatgrass can be effective at excluding cheatgrass following seeding on burned areas, and several researchers have prescribed seeding with non-native grasses to outcompete cheatgrass (Young et al. 1972, Whitson and Koch 1998, Cox and Anderson 2004, Reid et al. 2008, Davies et al. 2011a, Mealor et al. 2013). Crested wheatgrass germinates earlier in the year than cheatgrass, giving it a competitive advantage (Young and Allen 1997). Crested wheatgrass seedings do not always succeed, but once crested wheatgrass becomes established, it can crowd out cheatgrass through competitive exclusion (Stewart and Hull 1949). Over one million acres of sagebrush steppe in Nevada alone have been plowed and seeded with crested wheatgrass (Tueller 1989). Ewel and Putz (2004) argued that planting non-native species can be justified when economic benefits accrue, or ecological and socioeconomic needs are better met by alien species than natives. Reid et al. (2008: 28) went so far as to suggest that "the concept of pure native communities has become not only problematic, but it is presented with catastrophic challenges by cheatgrass." Non-native grasses are often used in post-fire seeding because their seeds are cheap and readily available (Brooks 2008b, Ott et al. 2019), while funding constraints and shortage of native seed stocks hamper the use of native grasses for revegetation (Jones 2000, Beyers 2004, Boyd et al. 2015).

Establishment of crested wheatgrass is sometimes poor due to competition from cheatgrass (Pellant 1994). Higher seeding rates of nonnative perennial grasses do not necessarily lead to higher perennial grass densities (Eisworth et al. 2009). Siberian wheatgrass has not been found to be a viable restoration method for cheatgrass-invaded grasslands (Mazzola 2008). Chambers et al. (2007: 142) found that crested wheatgrass sites were no more resistant to cheatgrass invasion than native sagebrush steppe, stating, "The susceptibility of *A. cristatum* sites to invasion by *B. tectorum* following overgrazing by livestock or other disturbances is likely to be just as high as for *Artemisia tridentata* sites in similar ecological settings."

The use of crested wheatgrass to increase resistance to cheatgrass invasions is counteracted by its negative ecological effects (D'Antonio and Thomsen 2004). Crested wheatgrass plantings support fewer nesting bird species and a significantly lower density of birds, mammals, and reptiles than do native sagebrush steppe communities (Reynolds and Trost 1980, Rockwell et al. 2021). Crested wheatgrass monocultures show a radical decrease in native songbirds; this begins to recover as grass seedings are invaded by sagebrush (McAdoo et al. 1989). Call and Maser (1985: 524) reported that crested wheatgrass plantings are of little use to sage grouse. According to Connelly et al. (1991), conversion of sagebrush to wheatgrass will likely result in sage-grouse population declines due to reduced nesting success. Urness et al. (1983) found the nutritional quality of crested wheatgrass suitable to sustain mule deer as a winter forage. Some cultivars of crested wheatgrass appear to be a preferred forage for black-tailed jackrabbits (Ganskopp et al. 1983). Overall, crested wheatgrass severely limits habitat function for many species of native wildlife, and, like cheatgrass, contributes to the loss of biodiversity. Ewel and Putz (2004) conceded that use of alien species for one purpose, erosion control being an example given, may result in poor recovery of native plants and wildlife.

Crested wheatgrass plantings result in long-term displacement of native plants, and much lower plant diversity and richness (Christian and Wilson 1999, Bakker and Wilson 2004). Beyers (2004) observed that post-fire aerial seeding with non-native grasses has often resulted in suppression of native vegetation. As crested wheatgrass invades native High Plains systems, cover and richness of native plants decrease, but individually Sandberg's bluegrass increases and blue grama remains unchanged (Heidinga and Wilson 2002). Crested wheatgrass not only suppresses the growth of native plants, but also self-facilitates its own persistence and dominance by changing soil microbes (Jordan et al. 2008). Crested wheatgrass plantings have much lower soil nitrogen sequestration than native grasslands in the Northern Plains (Christian and Wilson 1999). Crested wheatgrass can disrupt the arbuscular mycorrhizal fungi associations that native grasses depend on for nutrient uptake (Jordan et al. 2012). Gasch et al. (2016) found that crested wheatgrass continued to dominate reclaimed sites where it was seeded 11 to 29 years previously. The higher seed production an ability to produce seeds under a broader range of climactic conditions makes crested wheatgrass a superior competitor to the native bluebunch wheatgrass, giving it the characteristics of "an ideal weed" (Pyke 1990: 541). Frischknecht and Bleak (1957) argued that sagebrush will recolonize crested wheatgrass seedings. However, Davies et al. (2013) found that broadcast seeding of sagebrush in crested wheatgrass plantings was only effective after herbicide treatments to control crested wheatgrass.

Jordan et al. (2012) classified crested wheatgrass as a strong invader, capable of becoming a community dominant and forming nearly monotypic stands in invaded grasslands. Crested wheatgrass has competitive advantages over native bluebunch wheatgrass in having an expanded window of seed-set and greater seedling survival, enabling this species to spread into native grasslands and compete successfully with native bunchgrasses (Pyke 1990), thereby becoming an invasive weed in its own right. Crested wheatgrass tends to spread from seeded areas into adjacent habitats (Hull and Klomp 1967). Difficult to eradicate once established, crested wheatgrass is considered an invasive grass species that spreads into surrounding habitats from original plantings (Bakker and Wilson 2004). Once it spreads, it can choke out the native bluebunch wheatgrass (Hull 1971). High levels of crested wheatgrass control using glyophsate resulted in an increase in cheatgrass (Davies et al. 2013). Efforts to re-establish a diverse community of native plants in crested wheatgrass plantings have largely failed (Davies et al. 2013). Pehrson and Sowell (2011) reviewed the literature and found that fire, livestock grazing, and mechanical treatments were ineffective at eliminating crested wheatgrass and restoring native species, and mechanical treatments in particular led to annual grass expansion; these researchers recommended multiple courses of herbicide treatment.

Plots seeded with introduced species were characterized by low species diversity 33 years later (Bowles 2011). Jones (2014) suggested seeding with common wheat in cheatgrass-invaded areas to compete with cheatgrass without suppressing the recovery of native species post-fire. Barclay et al. (2004) found that while ryegrass seedings transitioned out after 5 years, they impaired the establishment of native forbs and grasses. Lavin et al. (2013: 1638) cautioned, "The introduction of crested wheatgrass (*Agropyron cristatum*) is considered as an impediment to the restoration of sagebrush steppe."

Similar results have been found for other non-native grasses planted to discourage cheatgrass dominance. Pyke (1990) found that non-native desert wheatgrass (*A. desertorum*) outperforms bluebunch wheatgrass in seed production, and outcompetes it, ultimately replacing the native grass. According to Barclay et al. (2004: 192), even when erosion is controlled by ryegrass plantings there is risk of non-native species introductions and may not be worth the delay in succession to native species.

Forage kochia (*Kochia prostrata*) has been introduced on over 200,000 hectares throughout the Intermountain West to provide fuelbreaks and livestock forage, and to compete with invasive plants (Gray 2011). Forage kochia has a higher plant moisture content in August than does crested wheatgrass and was also suggested as a fuelbreak planting (Pellant 1994). Both crested wheatgrass and forage kochia can disperse from a fuelbreak into adjacent habitats, displacing native plants (Shinneman et al. 2018, *and see* Pellant 1994). Gray (2011) found that kochia suppresses plant species richness in areas where it was planted and spread into neighboring habitats at 89% of sites sampled. Kochia is differentially invasive in low-lying depressions known as "slickspots," and suppresses the threatened plant slickspot peppergrass (Gray 2011).

Yet in emergency stabilization and rehabilitation settings, non-native seeding have been promoted as a quick and easy post-fire remedy. Seeding with non-native grasses and shrubs outperformed native seed mixes for establishing plant cover (Knutson et al. 2014). In post-fire seedings at large scales, crested wheatgrass and bottlebrush squirreltail did not significantly suppress cheatgrass, but Sandberg's bluegrass significantly suppressed cheatgrass once it reached a 5% cover threshold (Strand et al. 2017). Yet Sandberg bluegrass has not been used much in revegetation since it is low growing and not considered good livestock forage.

Cox and Anderson (2004) concluded that native perennial grasses had greater success after seeding in areas where crested wheatgrass had been planted as a hedge against cheatgrass (the concept of "assisted succession"), than when planted in cheatgrass-dominated areas. Brooks (2008a) pointed to plantings of crested wheatgrass as re-establishing more natural fire regimes to assist the return of native perennial bunchgrasses. However, at their Dugway Proving Ground site in Utah, while native grass seedings were more successful in crested wheatgrass during the first year, native plantings were equally unsuccessful in crested wheat and cheatgrass during the second year (Cox and Anderson 2004). Monsen (1994) concluded that crested wheatgrass seedings may help suppress cheatgrass but do not aid in returning plant communities to natural conditions.

Native Seedings

Seeding with native species has become the ecologically accepted standard in restoring disturbed areas to healthy native ecosystems, but this approach has a mixed record of success against cheatgrass invasions. Hoelzle et al. (2012) reported that seeding disturbed areas with native seed mix can result in dominance of perennial grasses 25 years later. Seeding Wyoming big sagebrush is effective after fire but is more successful where pre-fire vegetation was native plants than where cheatgrass monoculture dominated the site pre-fire (Eiswerth et al. 2009). Repeat applications of native seeds may be necessary to ultimately gain the upper hand over cheatgrass (Monaco et al. 2017).

Attempts to seed native grasses into cheatgrass monocultures have often failed due to the superior competitive ability of cheatgrass seedlings against perennial grass seedlings (Harris 1967). Seeding perennial grasses into cheatgrass without soil preparation tends to end in failure (Klemmedson and Smith 1964). Knutson et al. (2014) reported little success with aerial seeding of native grasses, but some success when native seeds were drill-seeded. Seeding burned areas with native plants did not affect cheatgrass abundance (Shinneman and Baker 2009). McGlone (2010) did not find any support for using native seedings to combat established cheatgrass infestations. Prevéy et al. (2014) documented little germination with broadcast seedings in Colorado shortgrass prairie. Aerial seeding with native species was associated with greater cover of cheatgrass in burn interiors (Getz and Baker 2008). Seedling performance for native grasses was higher in post-fire interspaces than in post-fire canopy sites, which burned with greater intensity (Boyd and Davies 2012). Gasch et al. (2016) found that vegetation cover was similar between sites reclaimed with crested wheatgrass and those reclaimed with native grasses.

Thirty-three years after disturbance, plots initially seeded with native species were dominated by native species, while plots initially seeded with introduced species (particularly crested wheatgrass) were still dominated by introduced species (Bowles 2011). According to Mack (2011), re-seeding with non-native species is steadily being replaced with native species, but the re-introduction of native species needs to be rapidly and substantially expanded in scope, in terms of number of species reintroduced, tonnage of native seeds collected and distributed, and the area of cheatgrass-dominated landscapes restored to native vegetation. Stromberg et al. (2007) recommended collecting the seeds from the same watershed as the disturbed site.

Perhaps due to the requirement of sagebrush seedlings for abundant moisture (Stahl et al. 1998), seeding of sagebrush into cheatgrass stands has met with limited success. Kulpa et al. (2012) found that seeded shrubs declined to near-undetectable levels within several years. Knutson et al. (2014) reported that seeding of sagebrush post-fire yields little result. According to Rowe and Brown (2008: 638), by contrast, both artificial seeding of sagebrush and natural seeding from nearby sagebrush were effective.

Chemical Herbicides

Herbicide treatments have met with some short-term success in suppressing cheatgrass but have yet to yield long-term recovery to native vegetation with a single treatment. Davies et al. (2012b) found some reduction of cheatgrass with herbicide application. Hirsch et al. (2012) found that herbicides were more effective in sagebrush than in salt desert communities. Viable seeds in the litter and soil allow cheatgrass populations to recolonize a site despite short-term herbicide treatments (Young et al. 1969). Seed production per plant increases with decreasing plant density in a compensatory manner, so thinning cheatgrass density with herbicide treatments does not necessarily reduce the seed bank available to repopulate cheatgrass the following year (Young et al. 1969). Roundy et al. (2007) found that disturbance through fire or herbicide treatment that killed perennial grasses did not have a major effect on cheatgrass germination, because soil and moisture parameters were suitable for cheatgrass germination on both treated and untreated sites. Seeds can remain viable for multiple years, allowing cheatgrass to escape herbicide treatments (Young et al. 1969). These factors explain why herbicide treatments often fail to yield long-term results and must be repeated frequently on the invaded area in question to achieve lasting results. In addition, side effects of large-scale herbicide spraying for cheatgrass can be severe. Postfire dust blowing tens to hundreds of kilometers, carrying herbicides used to fight cheatgrass along with it, affected downwind crop fields and spurred lawsuits that have discouraged the use of chemical herbicides for cheatgrass control (Germino et al. 2016).

A variety of herbicides have been used to combat cheatgrass infestations, including quizalofop, fluazifop, sethoxydim, atrazine (paraquat), glyphosate (RoundUp), imazameth, sulfometuron methyl, imazapic (Plateau), rimsulfuron (Matrix, Resolve), propoxycarbozone sodium, sulfometuron plus chlorsulfuron, sulfosulfuron, and indaziflam (Esplanade) (Carpenter and Murray 2004, *and see* Kaczmarski 2000, Mealor et al. 2013, Clark et al. 2019). In western Nevada, atrazine was effective at reducing cheatgrass, but broadleaf weeds invaded in the wake of this treatment, and cheatgrass persisted below the canopy of sagebrush shrubs killed by herbicidal treatment (Evans and Young 1977). Whitson and Koch (1998) found that atrazine and glyphosate could be effective at reducing cheatgrass when paired with livestock grazing. Young et al. (1969) achieved less-promising results, finding that atrazine generally reduced seed production for cheatgrass, but did not eliminate it. Treatments of atrazine plus fallowing eliminated cheatgrass plants but had little influence on seed production (Young et al. 1969). Currie et al. (1987) found that pronamide was the most effective herbicide at reducing cheatgrass and Japanese brome, while atrazine was the most cost-effective, and both increased the yield of perennial grasses post-treatment. Pellant (1996) suggested that sulfometuron methyl was an effective herbicide for cheatgrass, and Pellant et al. (1999) found that the use of sulfometuron methyl reduced cheatgrass and increased crested wheatgrass cover and vigor, at least for the first three years post-treatment. Shaw and Monsen (2000) reported that sulfometuron methyl treatments reduced cheatgrass production by 60-95% versus controls.

Hirsch et al. (2012) found that both imazapic and rimsulfuron were effective at reducing seedling emergence for cheatgrass. Anecdotally, imazapic has been used with success against cheatgrass infestations of 26-50% cover (Mealor et al. 2013). However, other researchers found that cheatgrass showed cover levels following imazapic treatment likely sufficient for the species to repopulate absent re-treatment (Baker et al. 2009). Imazapic application reduced cheatgrass by 7-90% when applied between early September and mid-October; application prior to seedling germination yielded poor results (Mangold et al. 2013). Owen et al. (2011) found that one-time treatment with imazapic and shrub seeding was only slightly effective at treating heavy cheatgrass infestations. Morris et al. (2009) found that imazapic was effective at reducing cheatgrass in the short term, but if abundant precipitation prevailed, the cheatgrass would return to pre-treatment levels within two years. Rau et al. (2014) documented that cheatgrass cover was significantly lower up to three years post-treatment with imazapic. Elseroad and Rudd (2011) found that treatment with imazapic reduced cheatgrass cover for 3-4 years but failed to spur expansion of perennial grasses. Lehnhoff et al. (2019) found that integrated use of either glyphosate, rimsulfuron, and imazapic with sheep grazing failed to reduce cheatgrass biomass or seed production in future years, because these treatments failed to increase native grass cover. Rau et al. (2014) found that imazapic treatment followed by prescribed fire reduced perennial grass cover, and Roundy et al. (2018) found that imazapic combined with burning resulted in cheatgrass expansion.

While imazapic can suppress cheatgrass, it can also suppress native perennial grasses (Rau et al. 2014). Baker et al. (2009) found that imazapic reduced cheatgrass cover by two-thirds, but also reduced native forbs by 84% and reduced two species of native grasses, Sandberg's bluegrass and slender wheatgrass. Imazapic also reduced shrub germination by 50-80%, while reducing cheatgrass cover by 20%, and reducing nontarget forb cover by 25% (Owen et al. 2011). Imazapic affected cheatgrass, crested wheatgrass, and squirreltail, while rimsulfuron had no effect on squirreltail (Hirsch et al. 2012). Heavy treatments with sulfometuron methyl caused yellowing and reduced growth for Sandberg's bluegrass and bottlebrush squirreltail (Shaw and Monsen 2000).

Indaziflam shows promise as a cheatgrass control herbicide and has limited effect on native species richness and abundance when used by itself (Clark et al. 2019). Indaziflam showed 89 to 94 percent reductions in cheatgrass 4 years after treatment when mixed with picloram, a broadleaf herbicide, plus imazapic and aminocyclopyrachlor

(Sebastian et al. 2017). However, applying indaziflam together with picloram had negative effects on native plant richness and abundance (Clark et al. 2019). Indaziflam kills the cheatgrass seedling as the root emerges from the seed, and this ability to render seeds nonviable gives this herbicide better promise for long-term cheatgrass control (Sebastian et al. 2016).

While herbicides alone may have limited long-term effectiveness in reducing cheatgrass, combining this with re-seeding of native species can yield improved results. Young et al. (1969) recommended seeding with native grasses in conjunction with herbicide treatments, so perennial grasses could take advantage of reduced competition from cheatgrass. According to Klemmedson and Smith (1964: 258), Herbicide treatments are not feasible over large areas, and are likely to be fruitless if not accompanied by reseeding of desirable grasses.

Soil Amendments

The addition of nutrients to the soil to affect cheatgrass populations has been the subject of much experimentation. Cheatgrass exerts severe competitive pressure on perennial grasses, and the addition of nitrogen to the soil increases this competition (Evans and Young 1977, Vasquez et al. 2008). Cheatgrass outcompeted blue grama when fertilized with high levels of nitrogen (Fenesi et al. 2011). Fertilization with nitrogen increased cheatgrass growth in the context of cultivated croplands (Rasmussen 1995). Rao and Allen (2010) experimented with varying levels of moisture and added nitrogen and found that cheatgrass and native forb growth response to added nitrogen was greatest at the highest level of moisture.

Because cheatgrass tends to thrive with abundant soil nitrogen and potassium, researchers have repeatedly attempted soil amendments designed to immobilize or reduce these soil nutrients as a method of cheatgrass control. Monaco et al. (2003) found that soil nitrogen shortages affected cheatgrass and native perennial grasses equally. Bowles (2011), by contrast, found that fertilizer treatments disproportionately favored introduced grasses over native species. On Southern Plains old-field succession sites, experimental addition of nitrogen to the soil increased annual grasses and forbs, while applications of sucrose to reduce soil nitrogen resulted in increases in perennial grasses (Paschke et al. 2000). In the Piceance Basin of Colorado, Bowles (2011) found that fertilizer treatment had short-term effects on the plant community, but effects became insignificant over time. In experimental treatments of disturbed a sagebrush community, McLendon and Redente (1992) found that plots treated with a sucrose treatment to reduce soil nitrogen availability had significantly less cheatgrass cover. Nitrogen reduction through the addition of sucrose resulted in decreases cheatgrass density in high-density stands (Beckstead and Augspurger 2004). However, Mazzola (2008) and Yoder and Caldwell (2002) found that artificially decreasing soil nitrogen had no long-term benefit for suppressing cheatgrass or increasing native bunchgrasses. Likewise, other soil treatments have shown equally little promise for cheatgrass control. Magnesium oxide soil amendments significantly suppressed cheatgrass establishment initially, but ultimately had no effect on the ultimate biomass of cheatgrass on treated plots (Miller et al. 2006).

Vesicular-arbuscular mycorrhizae (VAM) may need to be re-established on disturbed sites as part of site restoration (Stromberg et al. 2007). Mack (2011) recommended inoculating disturbed soils with biological soil crust propagules. In Rocky Mountain National Park, late-successional native plants responded positively to inoculation with arbuscular mycorrhizal fungi, and cheatgrass responded negatively, but commercial innocula were ineffective (Rowe et al. 2007). Inoculation of soils with VAM or using VAM-inoculated plants has had limited success (Wicklow-Howard 1994). Nitrogen amendments reduced VAM densities (Al-Qawari 2002). Condon and Pyke (2016) recommended "seeding" mosses to re-establish biological soil crust following disturbance, to inhibit cheatgrass invasion. High amounts of moss cover were achieved in the absence of irrigation, particularly with the application of jute netting. Soil microbe inoculum from cheatgrass-free sites and sucrose amendments to decrease nitrogen availability reduced cheatgrass cover and increased cover of native perennial grasses in heavily invaded settings (Rowe et al. 2009). This type of soil amendment deserves further study to see if its effectiveness can be replicated in a way that is scalable to large landscapes.

Natural Parasites

Smut fungi and a bacterium have often been proposed as biological controls for cheatgrass (e.g., Mack 2011). Head smut (*Ustilago bullata*), chestnut bunt (*Tilletia fusca*), and black-fingers-of-death (*Pyrnophora semeniperda*) are fungal pathogens that have been investigated as biological control agents to target cheatgrass (Meyer et al. 2008).

Head smut is vitually ubiquitous in cheatgrass populations, although epidemic levels (>30% smutted tillers) occur only sporadically, usually on mesic sites with reliable autumn precipitation (Meyer et al 2016). Warg (1938) documented smut outbreaks affecting cheatgrass at several-year intervals, but the cheatgrass soon re-established itself. Head smut infects the seedling and lives inside the vegetative tissues until the plant flowers, whereupon it attacks the seeds (Meyer et al. 2016). Mack and Pyke (1984) reported that head smut (*Ustilago bullata*) was an occasional cause of cheatgrass death but was only a minor cause of total mortality.

Pyrenophora semeniperda is a fungal seed pathogen of cheatgrass and has repeatedly been suggested as a biological control agent (Beckstead et al. 2007, Meyer et al. 2007). According to Smith et al. (2008), *P. semeniperda* may prevent annual carryover of much of the cheatgrass seed bank. It may also limit multi-year survival of cheatgrass seeds. According to Stewart and Young (1939: 1004), *P. semeniperda* was so abundant in 1935 and 1936 on the foothills north of Mountain Home, Idaho that cheatgrass seed production was heavily suppressed, relaxing competition with perennial grasses that remained sufficiently abundant to take advantage of the vacant niches that resulted. Non-dormant cheatgrass seeds sprout quickly and frequently escape *P. semeniperda* infection (Beckstead et al. 2007). Notably, *P. semeniperda* can also infect and kill native grasses (Beckstead et al. 2010).

Other pathogens also have been proposed for study as cheatgrass control agents. Chestnut bunt (*Tilletia fusca*) infects the seedling and interferes with seed production (Meyer et al. 2016). *Fusarium spp.* seed rot and bleach blonde pathogen (Rutstroemiaceae) also infect cheatgrass seeds and can have major impacts on seedling emergence and seed production (Meyer et al. 2016). The root-colonizing bacterium *Pseudomonas fluorescens* has shown some promise in suppressing cheatgrass root growth, but also affected some non-target grasses in one study (Kennedy et al. 2001). *P. fluorescens* was found to be completely ineffective at cheatgrass suppression in a second study (Tekiela 2019).

Unintended side effects could outweigh the benefits of these natural pathogens. Black fingers of death are not host-specific and might kill the seeds of native plants as well (Meyer et al. 2008). The development of microorganisms for the biological control of cheatgrass are hampered by the possibility that these organisms could pose a threat to commercial grain crops (Mack 2011).

Meyer et al. (2008) suggested that applying head smut, chestnut bunt, and black-fingers-of-death in concert would result in the greatest likelihood of cheatgrass suppression, and each have caused extinction or near-extinction of cheatgrass locally. Head smut epidemics can result in dominance of bunchgrasses, at least over small areas (Meyer et al. 2016). However, Klemmedson and Smith (1964) reported that while smut may temporarily reduce a cheatgrass stand, cheatgrass reestablishment is rapid. Garner et al. (2019: 101) expressed little hope for controlling cheatgrass with pathogens, citing a lack of evidence that fungal pathogens or bacterial agents were effective against cheatgrass. Smut infection rates of 17 to 23% were found to be ineffective at suppressing cheatgrass expansion (Beckstead and Augspurger 2004). According to Mack (2011), although cheatgrass can be locally controlled by herbivory and head smut together, complete control is not possible.

Targeted Livestock Grazing

Despite the strong connection between heavy livestock grazing and cheatgrass spread, targeted livestock grazing has repeatedly been suggested as a potential remedy for cheatgrass infestations (e.g., Pellant 1996). Rose and Miller (1994) argued that introduction of livestock has altered fire return intervals through removal of fine fuels that carry a fire once it is ignited. Some suggest that moderate grazing could reduce fuel loads and reduce risk and severity of fire, and that targeted grazing could be used to interrupt otherwise continuous fine fuels (Brooks and Chambers 2011, Davies et al. 2011a, Strand et al. 2014). Launchbaugh et al. (2008) recommended targeted, severe grazing over carefully planned areas. Garner et al. (2019) contended that targeted grazing with sheep can eliminate cheatgrass, but effects of targeted grazing are often cumulative and slow and still need to be tested for applicability across large areas. Diamond et al. (2012) found a short-term decrease in cheatgrass and increase in Sandberg's bluegrass as a result of the spring grazing/fall burning treatment applied. Sanders (1994) speculated that in high-precipitation zones (>14 inches annually), cheatgrass monocultures could be converted back to perennial grasslands using livestock grazing with ample seed source of native perennials, but that there would be little chance of such a conversion on drier sites. But because cheatgrass is grazing tolerant, the use of livestock to control cheatgrass is problematic (Pyke 2000). Goats and sheep that can be herded are more suited for targeted grazing than cattle, and small, fenced pastures are better than large open range situations (Goehring et al. 2010).

A number of studies contend that targeting cattle grazing at cheatgrass reduction is unworkable. In their Carrizo Plain study area, Kimball and Schiffman (2003) concluded that livestock grazing for restoration is counterproductive, harming native species and promoting alien plant growth. According to Young and Allen (1997), annual early spring grazing weakens cool-season perennial grasses and allows habitat for cheatgrass to increase. They assert the fact that excessive spring grazing both enhances the presence of and biologically suppresses the abundance of cheatgrass as one of the most misunderstood aspects of the biology of this grass. Grazing just after flowering and prior to seed formation (during the early onset of purple coloration) can damage or kill cheatgrass plants and inhibit cheatgrass seed production (Vallentine and Stevens 1994). However, Kaczmarski (2000) argued that grazing is ineffective at controlling cheatgrass, because cheatgrass regenerates and can set seed following spring grazing, and because plants grazed in fall or winter have already set seed. This allows cheatgrass to escape grazing pressure in seed form and sprout again the following autumn or spring. Mayer et al. (2013: 4) pointed out that there is a lack of rigorous/credible scientific studies on the targeted livestock grazing's effect on cheatgrass.

However, some studies have found that cattle herbivory decreases *B. tectorum* abundance (*e.g.,* Hempy-Mayer and Pyke 2009). Launchbaugh et al. (2008) contended that grazing by cattle late in the growing season or over the winter reduces residual herbaceous biomass, thus livestock grazing can potentially affect fire behavior. However, Davies et al. (2015) found that winter grazing reduced overall herbaceous cover and continuity by 40%, and reduced perennial bunchgrass biomass by 58%, but did not change annual grass biomass, indicating that cattle avoided eating cured cheatgrass. However, properly timed grazing on cheatgrass in the spring stimulates tillering and thereby increases the harvestable forage from the species (Young and Clements 2007). Intensive grazing (80-90% removal over a 32- to 40-hour period) plus fire resulted in near-term reductions of cheatgrass cover (Diamond et al. 2010, 2012). After two years of targeted grazing, cheatgrass seed bank densities were reduced, but remained well above the 330 seeds per square meter threshold required for successful native seedling establishment (Diamond et al. 2012).

Heavy grazing can reduce fuels associated with senescent cheatgrass stands in the short term. Schmelzer et al. (2014) reported that with 58-80% utilization, standing crops of cheatgrass were reduced below 45 kg/acre, the threshold that supports the most extreme fire behavior. Davies et al. (2015) argued that less biomass due to winter grazing could lead to decreased severity of fires. Davies et al. (2021) documented reduced fire intensity on grazed versus ungrazed pastures treated with prescribed fire, although the late-September temperatures of 22.8°C (73°F) to 27.2°C (81°F) are not representative of the extreme fire weather when large range fires tend to occur. Under extreme fire conditions (low fuel moisture, high temperatures, and gusty winds), moderate grazing has limited or negligible effects on fire behavior (Lauchbaugh et al. 2008). Davies et al. (2015) hypothesized that ungrazed shrubsteppe contained more finer fuels, and would be dry enough to burn by mid-June to early July, while winter grazed areas were unlikely to burn until late August. Diamond et al. (2010) found that spring grazing on cheatgrass could result in reduced flame lengths for prescribed fires in October. Under moderate fire conditions, grazing may reduce the intensity and spread of fires (Launchbaugh et al. 2008).

Under extreme fire weather, livestock grazing and reduced fuel loads have little effect on fire dynamics (Strand et al. 2014). When there is less than 12% dead fuel moisture, and winds were greater than 15 mph, previous grazing has little effect on fire behavior (Launchbaugh et al. 2008, Diamond et al. 2010). Also, the high-intensity grazing required to reduce fire risk can have negative long-term results. According to Diamond et al. (2010: 949), "A moderate level of utilization is a standard grazing management prescription for most semiarid rangelands in the western USA; therefore, reducing herbaceous biomass to levels that would strongly influence fire behavior under extreme fire conditions would require reductions that would potentially degrade shrub and grassland communities, and compromise sustained livestock production." There appears to be a consensus that grazing for fuels reduction has no measurable benefit under extreme fire weather conditions.

The heavy level of livestock grazing required to decrease cheatgrass abundance eliminates the remaining native grasses, which are more palatable, perpetuating and expanding cheatgrass dominance in future years. While cheatgrass may decline under heavy grazing pressure, it can withstand heavy grazing better than perennial grasses (Klemmedson and Smith 1964). Heavy spring livestock grazing for fuels reduction can be detrimental to native plants and soil crusts, and the heavy grazing required to achieve fuels reduction can accelerate the spread of other noxious weeds (Pellant 2000). Under 58 to 80% forage utilization, Schmelzer et al. (2014) reported no short-term decrease in perennial grass (particularly crested wheatgrass) abundance, although the need for longer-term monitoring of continued grazing was noted. Spring grazing of cheatgrass led to an increase in halogeton (DeFlon 1986), which is also an undesirable, non-native weed. Spring grazing alone reduced cheatgrass cover slightly, but increased cover of other invasive plants such as tumblemustard (Diamond et al. 2012). Heavy cattle grazing significantly reduced cheatgrass seed density in the seedbank, but seed density remained at 1,754 plants/square meter, far above the density needed to return the site once again to a cheatgrass dominance (Schmelzer et al. 2014). Young and Clements (2007: 19) pointed out that spring grazing for cheatgrass control further damages residual perennial grasses: "Once the cheatgrass is mature, the still green native perennial grasses are selectively overgrazed by cattle. If the density of native perennials is low, even low levels of trespass grazing are sufficient to selectively over-utilize the native perennial grasses."

In the long term, livestock grazing has shown no ability to reduce or eliminate cheatgrass. Briske et al. (2013: 73) concluded that grass cover increases dramatically with rest, and that intensive grazing delays this recovery. Mack (2011) asserted that livestock grazing was incapable of destroying a cheatgrass population. As Young and Clements (2007) pointed out, early spring, when cattle are turned out onto western rangelands, is when native perennial grasses are most susceptible to harm, while cheatgrass is less vulnerable to grazing-related damage at this time of year.

According to Vallentine and Stevens (1994), with limited exceptions, grazing is not an effective tool for cheatgrass control. According to Carpenter and Murray (2005: 17), "grazing is not a recommended method of control for cheatgrass. If the plants are grazed in the spring, they will regenerate new culms and produce additional seeds. When grazed in the summer or fall the plants will not regrow, but by then viable seeds have already been produced." Biomass removal, simulating grazing, did not decrease cheatgrass density for areas already dominated by cheatgrass (McGlone et al. 2010). Reisner et al. (2013) found no support for the idea that cattle grazing reduced cheatgrass invasions, and, to the contrary found that heavy grazing promoted the magnitude of cheatgrass dominance.

Pellant (1990: 13) considered livestock grazing on cheatgrass a useful fire pre-suppression tool if livestock numbers were carefully manipulated to harvest extremes of annual grass production, and monitoring could ensure that remnant perennial species are not lost. Mealor et al. (2013) reviewed several studies finding cheatgrass reductions as a result of targeted grazing but concluded that insufficient evidence existed to prescribe targeted grazing for long-term reduction of cheatgrass infestations. Given the size of recent wildfires relative to the size of areas where high-impact grazing can successfully be implemented, applicability is likely limited to fuelbreaks or property protection (Chambers et al. 2016). However, Shinneman et al. (2018) dismissed targeted grazing as a means of creating fuelbreaks, because it is applicable only to limited and novel situations on degraded lands with low resistance to invasion and high cover of exotic annual grass.

In order for targeted grazing to succeed in reducing fire risk, grasses must essentially be grazed down to bare soil. The 80-90% forage utilization required to achieve fuels reduction also negatively affects native grasses, leading to their decline or loss (Jones and Carter 2016). Because of the level of biomass removal required for reducing fire risk, targeted grazing must be used with caution and only on degraded sites with little to no perennial cover (Diamond et al. 2010). Young et al. (1987: 267) observed, "Green forage is at a premium earlier in the year in March and April. During this time cheatgrass consists of seedlings or prostrate rosettes of virtually no harvestable forage production. In contrast, perennial grasses, both native and introduced, have greened up and grown enough to provide some early spring forage. Unfortunately, this is the time of year when native perennial grasses are most susceptible to damage from repeated grazing, which depletes the carbohydrate reserves needed for flowering."

The high-intensity grazing required to reduce cheatgrass sufficiently to affect fire behavior under extreme fire conditions tends to be ecologically damaging. Loeser et al. (2007) found that high-impact, short duration cattle grazing resulted in cheatgrass expansion and dominance, particularly in combination with extreme drought. Chambers et al. (2016) found that herbivory's negative effects on cheatgrass can be exceeded by the negative effect of the removal of native grasses and forbs which are preferentially selected by herbivores. Launchbaugh et al. (2008) stated that effectively influencing fire behavior through grazing would necessarily result in biomass removal that is not sustainable and may compromise the health of the ecosystem. Reductions in fuels due to livestock may reduce fire frequency in mountain big sagebrush habitats but may also lead to pinyon-juniper expansion (Brooks et al. 2015). With heavy enough disturbance, cheatgrass can be suppressed to encourage the growth of Russian thistle, itself a noxious weed (Young et al. 1972).

Thus, heavy livestock grazing can reduce fine fuels associated with cheatgrass, which translates into reductions in fire risk during moderate fire weather but has little effect during extreme fire conditions when the largest and most severe fires occur. Heavy levels of livestock grazing, 80-90 percent, are required to make a measurable difference in fuel loads, but these levels of forage removal are linked to continued loss of native bunchgrasses and increasing the dominance of cheatgrass. With these considerations in mind, the modest, short-term benefits of targeted livestock grazing are strongly outweighed by the long-term drawbacks of native plant loss and entrenchment of cheatgrass dominance, making targeted livestock grazing a counterproductive strategy to address cheatgrass infestations.

Prescribed Fire

Prescribed fire, particularly prior to seed maturation, was at one time suggested as a method of cheatgrass control. Removal of herbaceous perennials using herbicides increase soil water and nitrate availability but burning without removal have only minor effects (Chambers et al. 2007). Jones (2015) reported that repeated burning decreased cheatgrass abundance, by eliminating organic litter. This lack of litter may decrease the germination rates for cheatgrass but it can also increase erosion and encourage other noxious weeds. Mealor et al. (2013) recommended using prescribed fire in rare circumstances during the spring growth period. Young et al. (1987) asserted that hot fires burn all cheatgrass seeds in the seedbed, eliminating the species. However, prescribed fires are typically set during cool, moist weather when such hot fire temperatures would be difficult to attain. Lesica et al. (2007) recommended prescribed fire as a possible management tool in mountain big sagebrush, but not basin or Wyoming big sagebrush. Pellant (1996: 11) observed that burning during any season would only reduce, not eliminate, cheatgrass. Fire is unlikely to result in long-term reduction in cheatgrass because sufficient seeds are likely to survive to repopulate the burn over time (Rice and Smith 2008).

Rice and Smith (2008) pointed to some examples of success with burning in combination with use of certain herbicides, or seeding with perennial grasses. Prescribed fire followed by imazapic treatment in Utah resulted in reduced cover of cheatgrass and increases in perennial grasses, but these gains were short-lived due to abundance of cheatgrass seeds in the seed bank (Call 2013). In Wyoming big sagebrush communities that are resilient and dominated by native species, fire can create fuelbreaks to contain future conflagrations (Reis et al. 2019). Fall burning alone did not have lasting effects on cheatgrass populations, as cheatgrass populations returned to pre-burn levels within one year (Diamond et al. 2012). The use of fire to eliminate cheatgrass by depleting soil nitrogen failed due to the failure of relatively low-temperature cheatgrass fires to alter soil nitrogen banks (Jones et al. 2015).

Several studies highlight the risks and costs of prescribed fire as a cheatgrass-reduction tool, particularly in pinyon-juniper woodlands. Meyer et al. (2008) pointed out that early season burning, fall tilling, and herbicide use tend to be risky, expensive, or damaging to remnant perennial vegetation. Prescribed fire in late successional juniper woodlands is sufficiently hot to kill most perennial bunchgrasses, favoring cheatgrass dominance post-fire (Bates et al. 2011). Prescribed fire in pinyon-juniper expansion areas resulted in the greatest increase in cheatgrass (Roundy et al. 2018).

Applying prescribed fire in cheatgrass-infested areas poses a strong risk of exacerbating the infestation. Burning after cheatgrass seeds mature has little effect on subsequent stands, because cheatgrass seeds survive fire well (Klemmedson and Smith 1964). West and Hassan (1985) recommended applying prescribed fire in rangelands in good condition, because the elimination of sagebrush and increase of cheatgrass would result in greater forage production for livestock following at least two years of rest. By promoting prescribed fire as a means to stimulate cheatgrass production, this recommendation is perhaps the most scathing indictment of the use of prescribed fire as a means of cheatgrass suppression.

Fuel Breaks, Green Strips, and Fire Suppression

Shinneman et al. (2018) defined 'fuel break' as a type of fuel treatment that involves the removal or modification of vegetation in strategically placed strips or blocks of land, specifically to disrupt fuel continuity and reduce fuel loads and accumulation. Fuel breaks are designed to create safe and strategic anchor points for firefighting crews and to compartmentalize fires to constrain their expansion (Shinneman et al. 2018). Most fuel breaks in non-forested areas are at most 100 yards wide, and although wider fuel breaks are considered better for altering fire behavior under more extreme conditions, it is impractical or unrealistic to create excessively wide fuel breaks over many linear kilometers (Shinneman et al. 2018).

Greenstripping, the clearing and planting of firebreaks, was first instituted in California in 1957 (Pellant 1990). The greenstripping program with strategically placed fuel breaks 30 to 400 feet wide was instituted in Idaho by the Bureau of Land Management (BLM) in 1985, and planting crested wheatgrass along roadways to create firebreaks was underway as early as 1981 (Pellant 1994). Idaho BLM initially constructed 199 miles of fire line (Pellant 1990), and 451 miles of greenstrips were planted in Idaho from 1985 to 1993 (Pellant 1994). Based on a broader survey of GIS information, Shinneman et al. (2018) determined that there are already at least 10,000 linear kilometers of fuel breaks in the Great Basin, encompassing over 330,000 acres of disturbed area. Fuel breaks have been constructed since the early 1990s, with at least 143,000 acres of fuels treatments on BLM lands recorded in the Fire Treatments Effectiveness Monitoring Program, yet records are too sparse and difficult to analyze to systematically determine the relative effectiveness of these fuel treatments (Shinneman et al. 2018). Pellant (1996) advised that greenstripping is not the solution to the 'cheatgrass-wildfire' cycle, but rather it is another tool to help reduce the size and frequency of wildfires. Notwithstanding this analysis, there is little evidence that the extensive and previously constructed system of greenstrips and fuel breaks that has existed for the past sixty years has made a decisive difference in fire size or spread.

Greenstrips typically use non-native grasses and subshrubs, including crested wheatgrass, Russian wildrye, Siberian wheatgrass, and forage kochia (Pellant 1990). Fuel breaks are sometimes planted with non-native plant species that better retain water later in the season (often crested wheatgrass or forage kochia), can be bladed down to bare mineral soil to remove all plants, or mowed to eliminate shrubs and reduce fuel heights (Shinneman et al. 2018). Mowing can create a fuel break but in some soil types and terrain the mowing creates a great deal of soil disturbance and thus promotes more cheatgrass. However, non-native species intentionally seeded in greenstrips can invade surrounding undisturbed habitats (Shinneman et al. 2019), becoming invasive weed problems in their own right.

Pellant (2000) continued to endorse greenstripping to limit fire spread, although he tempered his enthusiasm by noting that the success of greenstrips in combating fire is poorly documented. Monsen (1994) argued that greenstrips in cheatgrass monoculture can reduce the incidence of large fires. Maestas et al. (2016) suggested that sage grouse priority habitats with low resilience and resistance to weed invasion should be the priority for fuel break construction in advance of potential fires but did not suggest that livestock grazing should be reduced to foster the resilience of native ecosystems through maintaining native bunchgrasses and biological soil crusts. According to Pellant (1990), fuelbreaks are ineffective in rocky areas, prone to erosion and noxious weed invasion, and are visually obtrusive.

Without regular maintenance, fuel breaks can become vectors or corridors for weed invasion, particularly greenstrips where bunchgrass seedings fail, and bladed strips not treated regularly for weeds (Shinneman et al. 2018, 2019). Anecdotally, according to Vollmer (2005), fuel breaks that are left untended can become fire hazards in their own right when they are invaded by annual weedy species and cheatgrass, acting as a wick for spreading fire into new areas. Bureau of Land Management personnel commonly refer to these fuel breaks where the seeding of perennial grasses failed as "weed corridors" (pers. comm., Signe Sather-Blair, former Bruneau Field Office manager). Off-highway vehicle travel these failed fuel breaks and spread cheatgrass and other weeds into other areas.

The construction of fuel breaks and firelines could lead to increased soil nutrient availability because plants are removed, resulting in lowered nutrient uptake by plants (Brooks 2008b). Martinson et al. (2008) concluded that mechanically constructed fuel breaks can promote the spread of invasive plants, particularly cheatgrass.

The ability of fuel breaks to slow or contain fires remains undemonstrated, even after many decades of implementation. Some areas reported to have stopped wildfires have actually been areas where firefighters set back fires from these areas due to favorable winds. There is a scarcity of rigorous scientific testing regarding the effectiveness and the ecological impacts of fuel breaks (Shinneman et al. 2019). Anecdotally, greenstrips can help stop fires when paired with direct fire-suppression efforts (Pellant 1990). Pellant (2000) observed that some greenstrips were effective in reducing or stopping fire spread, especially in conjunction with roads, while others became dominated by cheatgrass and were readily breached by fires. According to Shinneman et al. (2018), there is some anecdotal evidence that indicates some fuel treatments may be effective, but inadequate data collection and limited record keeping are obstacles to conclusively assessing their effectiveness or their ecological impacts. One fuel break created by intensive grazing by domestic sheep did burn in a subsequent range fire event (Diamond et al. 2010). Fuel break effectiveness continues to be a subject of debate, yet relatively little research has tested the role of fuel breaks in constraining wildfire size and frequency (Maestas et al. 2016). While there are anecdotal reports of fuel breaks stopping fires, at least along significant parts of their length, there is a lack of empirical validation for overall effectiveness of fuel breaks as a means of reducing fire spread (Shinneman et al. 2018).

A number of negative ecological impacts of fuel breaks have been identified. Fuel breaks fragment wildlife habitats and can concentrate predators and serve as travel corridors (Shinneman et al. 2019). Shinneman et al. (2018) concluded that fuel breaks come with known ecological costs that convert hundreds of thousands of acres of habitat directly and affect millions of acres of adjacent habitat through edge effects and habitat fragmentation, for speculative benefit in containing severe fires during the extreme fire weather conditions when they are most likely to occur. Fuel breaks fragment sagebrush habitats and increase edge effects, which is problematic for sage grouse, sagebrush songbirds, and other wildlife (Shinneman et al. 2018). Graham (2013) documented that sage grouse avoid habitats fragmented by fuel break creation. According to Shinneman et al. (2019), land managers are actually increasing the fragmention of sagebrush habitat when they install fuel breaks.

Firefighting efforts and post-fire rehabilitation also have the potential to increase future cheatgrass infestations. According to Ponzetti et al. (2007: 719), the physical disturbance from fire-line plowing is more damaging to soil crusts than the fires themselves. Fire retardant supplies nitrogen and phosphorous to the soil, and therefore might also stimulate the spread of invasive species, although studies have yet to investigate this possibility (Zouhar et al. 2008). Ellsworth et al. (2016: 9) observed that fire suppression alone will not restore sage grouse habitat and may ultimately result in habitat degradation over the long term; allowing some fire in areas where post-fire environments facilitate native species recovery could help create future ideal habitat for sagebrush wildlife. The addition of carbon to the soil post-fire, such as hydromulch, hay, or chipped wood, can reduce availability of soil nutrients and shade the soil, may inhibit invasive weed germination (Brooks 2008b). However, Backer et al. (2004) cautioned that the ecological effects of fire suppression and post-fire rehabilitation work can be greater than the impacts of the fire itself.

Considering the certainty of habitat fragmentation and other negative ecological consequences, the significant risk of accelerating cheatgrass invasion and transmission when fuel breaks and greenstrips are inevitably neglected through lack of funding to maintain them, and the deeply questionable effectiveness of fuel breaks and greenstrips at stopping or even slowing fires (particularly during extreme fire weather), fuel breaks and greenstrips are likely to be a waste of effort and funding at best, and a counterproductive enabler of weed invasion at worst. The construction of fuel breaks should be limited to the course of actual fires, when strategic placement can at least assure the best chance at usefulness in containing the fire. Aggressively working to contain and extinguish fires is warranted when fires burn in cheatgrass-prone habitats, and in these areas, direct attack of fires in arid western rangelands remains the preferred approach.

Physical Disturbance

Historically, disking or plowing, or burning in early summer before cheatgrass seed heads mature, was suggested as a treatment for heavily infested areas (Pellant 1996). Klemmedson and Smith (1964) reported that the most effective method of eliminating cheatgrass prior to seeding with perennials is moldboard plowing. This is very expensive, however, and is not always feasible. Reducing cheatgrass through plowing or disking and planting with perennial grasses has achieved some success, but at significant expense (Stewart and Hull 1949). Nelson et al. (1970) reported that plowing and herbicides reduced cheatgrass competition with seeded bunchgrasses. Madsen et al. (2012) experimentally simulated tilling with anchor chains and application of surfactant wetting agents on post-fire soils. Wetting agents produced the greatest soil moisture and seedling growth and survival for both cheatgrass and crested wheatgrass, while tilling performed less well, and tilling together with wetting agents did not increase grass production versus wetting agents alone. Mowing and cutting are not recommended methods of control, and hand-pulling of cheatgrass is labor-intensive and only practical on very small infestations (Carpenter and Murray 2004). Prevéy et al. (2014) tested spring mowing and planting with native seeds to reduce cheatgrass infestations in the shortgrass prairies of eastern Colorado, and found that this treatment reduced cheatgrass, but increased invasive forbs.

Young et al. (1969) found that tillage had a variable effect on cheatgrass seed production, sometimes reducing it, sometimes enhancing it, depending on location. Disking was ineffective at controlling cheatgrass and resulted in even more cheatgrass than the control plots (Pellant et al. 1999). After the area was treated with tilling, harrowing, or glyphosate herbicide, native perennials generally re-established in crested wheatgrass plantings but not cheatgrass-dominated areas (Cox and Anderson 2004). According to Madsen et al. (2012: 187), restoration treatments intended to treat soil water repellency can also promote the establishment of cheatgrass and other invasive weeds.

Mowing of sagebrush, both alone and paired with drill-seeding of native perennial grasses, increased cheatgrass cover (Davies and Bates 2014). Mowing of sagebrush has been found to increase cheatgrass significantly, without increasing the productivity of perennial grasses (Davies et al. 2011b). Mowing also decreases moss, an important biological soil crust component (Davies et al. 2012a), which retards cheatgrass establishment. Cheatgrass plants were generally killed by mowing when cut near the ground when seedheads began to mature, but the seeds are already viable by this time (Hulbert 1955). Native perennial bunchgrasses did not respond to mowing in degraded Wyoming big sagebrush communities, but cheatgrass expanded 3.3-fold with mowing (Davies et al. 2012a).

Condon et al. (2011) counseled that introducing disturbance to more xeric sites will likely lead to increased cheatgrass dominance and should be avoided. Mowing degraded Wyoming big sagebrush elevated the fire risk through fostering cheatgrass expansion (Davies et al. 2012a). Overall, mowing and disking in areas with a significant cheatgrass components is largely discredited today as a restoration strategy.

Reduction of Livestock Grazing

Some researchers have proposed reductions in livestock grazing as a means to slow or reverse cheatgrass infestations. Plant communities can recover from cheatgrass dominance over time, particularly when grazing is lessened or eliminated (Bagchi et al. 2013). According to Garner et al. (2019), proper livestock management is crucial for maintaining native vegetation and biological soil crusts, which in turn ensure resistance to invasive plants. Davies et al. (2009) suggest that light to moderate grazing can reduce the magnitude of cheatgrass invasion. However, the return of native perennials through light grazing is slow (Cook and Harris 1952). DiTomaso (2000) recommend moderate grazing levels to minimize the physiological impact on native plants and to reduce soil disturbance as one of three methods to use grazing to combat invasive weeds. Grazing reductions can also yield positive metrics of post-fire recovery: Reducing livestock grazing intensity before fire occurs, along with using native seed mixes after fires in areas vulnerable to invasion could provide a more effective strategy for controlling cheatgrass invasion after fire (Shinneman and Baker 2009).

Boyd et al. (2014) postulated that heavy livestock grazing diminished perennial bunchgrasses and promoted the establishment of cheatgrass, but moderate levels of livestock grazing can be consistent with maintaining native bunchgrasses. Loeser et al. (2007) contended that intermediate levels of grazing may inhibit cheatgrass expansion, but in the long-term, removal of cattle may be more beneficial to native plant communities. Acceptable levels of grazing range from 25-35% annual plant removal in salt desert shrublands to 50% for shortgrass prairie with a long history of grazing (Holechek et al. 2010). According to Pyke et al. (2016: 329), light stocking levels and grazing seasons that allow seed and tiller production of perennial species are likely to increase resilience, especially for grass species that did not evolve with repeated grazing.

The definition of moderate levels of grazing is a matter of some scientific dispute. Boyd et al. (2014) stated that light to moderate levels of grazing (up to 50% forage utilization) would be compatible with maintaining bunchgrasses. Crawford et al. (2004) defined "moderate" grazing as 40-60% forage utilization and asserted that this level of grazing was compatible with maintaining perennial bunchgrasses. Strand et al (2014) argued that grazing at 50% utilization or less in early Spring or fall after senescence of native bunchgrasses does not accelerate cheatgrass invasion, while grazing over the summer and at utilization levels greater than 50% suppresses native bunchgrass, facilitating the expansion of cheatgrass. However, even lesser levels of livestock grazing can result in adverse ecological shifts. Because cheatgrass dries earlier than perennials, grazing animals will selectively graze the perennial grasses and avoid the dry cheatgrass (Stewart and Hull 1949). In the Chihuahuan Desert of New Mexico, annual grasses increased while perennial sod-forming grasses decreased under livestock grazing with as little as 30% forage removal (Lightfoot 2018). Livestock grazing managed for 30% forage removal changed grasshopper species assemblages, causing some species to increase and others to decrease (Lightfoot 2018). As a general rule, several researchers have recommended limiting livestock grazing to 25 to 35% forage removal on arid western rangelands (Galt et al. 2000, Holechek et al. 2010). Yet federal agencies typically permit 50% or more forage utilization on federal lands leased for livestock grazing, a level that does not account for exceedances because of grazing trespass, which remains a profitable option for ranchers given lax enforcement and nominal fine levels (Tal 2009).

Yeo (2005) found that livestock grazing at moderate levels suppressed bluebunch wheatgrass (*P. spicata*) and led to its replacement by low-growing Sandberg bluegrass (*Poa secunda*). Schmelzer et al. (2014) hypothesized that moderate (rather than heavy) grazing intensities, rather than heavy grazing itself, has fostered cheatgrass dominance in areas with existing infestations. Strand et al. (2014) suggest that reduced livestock grazing rates in recent decades have resulted in an increase of standing biomass, exacerbating range fires. Jones and Carter (2016) refute the findings of Davies et al. (2014) that light to moderate livestock grazing is ecologically equivalent to rest from livestock.

The timing of grazing can alao make a difference. Laycock (1967) stated that heavy spring grazing by sheep degrades sagebrush steppe, while fall grazing restores degraded plant communities better than rest from grazing.

While rotational grazing systems have sometimes been prescribed as a cheatgrass-reduction tool, there is little evidence supporting their effectiveness. Ranchers have blamed the spread of cheatgrass on deferred grazing systems (Young et al. 1987).

According to Mayer et al. (2013), there is a lack of institutional or informational support to determine proper post-fire grazing management, to understand the utility of grazing for fuels reduction in fire-prone habitats, and how to manage grazing to retain resilience in a pre-fire understory vegetation community.

A light-to-moderate stocking density maintains diverse plant assemblage with a dense root system, enabling increased carbon sequestration, according to Jones and Donnelly (2004). However, carefully managed grazing cannot achieve the carbon sequestration benefits of complete livestock removal. In southern Idaho, Root et al. (2020) found that heavy grazing pressure damaged biocrusts and led to an increase in the cheatgrass cover. Even moderate levels of livestock grazing can prevent recovery of biological soil crusts after heavy livestock grazing (Kaltenecker et al. 1999). Nonetheless, reductions in grazing intensity have excellent promise as a preventative measure to preclude new incursions of cheatgrass into relatively healthy, resilient, and cheatgrass-resistant areas.

Cessation of Livestock Grazing

Livestock removal is an effective approach to ecological restoration, benefitting soils, plants, and hydrology (Kaufmann et al. 2004). Hartway and Mills (2012) found that livestock exclusion was the most effective treatment at increasing nest success for threatened, endangered, or declining birds. Livestock exclusion increases animal diversity across all trophic levels except detritovores, but herbivores, predators, and pollinators benefit particularly (Filazzola et al. 2020). Parker et al. (2016) conducted a meta-analysis of 63 field studies using herbivore exclusion and found that native herbivores strongly suppressed the abundance of exotic plants, while exotic herbivores increased the abundance and richness of exotic plants. On the Dugway Proving Ground in central Utah, where domestic livestock have been absent and wild horses and pronghorns are only occasional visitors, cheatgrass had yet to extensively invade as of the turn of the 21st Century (Meyer et al. 2001). Yeo (2005) contended the health of semiarid ecosystems can improve with livestock exclusion, despite improved grazing management over the past half century. The reason that this obvious tool for cheatgrass reduction has not been frequently employed comes down to a matter of dollars and cents: “Long periods of complete rest are not usually an economical [sic] acceptable form of rangeland rehabilitation” (McLean and Tisdale 1971: 184).

The Idaho National Laboratory (INL), which was established for atomic energy research, includes a grazing exclosure 1,000 km^2 in extent (Germino et al. 2016), and makes a useful case study in the effects of grazing cessation on a large scale. According to Lavin et al. (2013), INL was heavily grazed during the early 1900s but generally closed to grazing since about World War II, and there are currently large tracts of biodiverse high-native-cover sagebrush steppe creating something of an accidental wilderness. Some 43% of INL (or 572,049 acres) has been closed to livestock grazing since at least 1957 (Anderson and Inouye 2001). Taylor et al. (2014) reported that their INL study site had not been grazed since the 1940s. INL was heavily degraded by sheep grazing prior to its establishment (Anderson and Holte 1981, Moritz 1988). Despite this, cheatgrass was rare at INL in 1950 (Anderson and Inouye 2001). In 25 years of rest from grazing at the Idaho National Laboratory, shrub cover increased 54%, while perennial grass cover increased twenty-fold (Anderson and Holte 1981). INL went from dense sagebrush with depleted perennial herbaceous understory to open stand of sagebrush with productive herbaceous perennial understory, in the context of favorable precipitation patterns, in the 25 years following removal of livestock (Anderson and Inouye 2001). In the absence of livestock on INL test plots, perennial grass increased thirteen-fold from a starting point of 0.5% cover between 1950 and 1975 (Anderson and Inouye 2001). Anderson and Inouye (2001)

Left: *Photo taken in 2023 after 8 years of recovery within a fenced exclosure created to exclude cattle by a landowner in Contact, Nevada in 2015. No native seeds were planted; the only change was cessation of livestock grazing (native herbivores were able to enter the exclosure). This change enabled substantial recovery of bluebunch wheatgrass, squirreltail, and Indian ricegrass.* ***Right:*** *Photo taken the same day on adjacent Bureau of Land Management lands grazed by cattle, showing cheatgrass dominance and an absence of native bunchgrasses. Erik Molvar photos.*

reported that cheatgrass averaged 2.3% cover in 1995 on INL, while native perennial grasses averaged almost 5.6% cover. Cheatgrass is widely present in ungrazed portions of INL, but at low levels of cover (Taylor et al. 2014). INL plots with very light or no livestock grazing have abundant native bunchgrasses and sparse occurrences of cheatgrass (Hoover and Germino 2012). Not all of INL is ungrazed by livestock, however, and Moritz (1988) reported up to 37.2% canopy coverage of cheatgrass in his INL burn areas.

Over time, biological soil crusts also recover from grazing-related disturbance. Protection from grazers for 15 years resulted in increased cover of biological soil crust (Rice and Westoby 1978). Duniway et al. (2018) documented a soil lichen recovery rate of 1 to 4% per year because of grazing removal. At these rates, full recovery would take 25 to 100 years. Areas grazed by sheep supported only 22% of the areal cover of biological crust that was present in ungrazed exclosures and contained only 25% of the soil crust species per unit area as ungrazed plots (Anderson et al 1982).

Specific to low-resilience Wyoming big sagebrush, Chambers et al. (2014: 371) recommend to close or actively control wild horse and cattle grazing to prevent loss of perennial native grasses and forbs and allow natural regeneration. Stewart and Hull (1949: 71) found that on plots without livestock and rabbits, perennial grasses increased about as rapidly as cheatgrass, but native species tended to disappear where grazed by both livestock and rabbits. Species diversity and richness were greatest at the ungrazed site (Concilio and Loik 2013). Ten native grasses were found in a canyon left ungrazed for 40 years that were completely absent in a neighboring, heavily grazed canyon (Cottam and Evans 1945).

Because exclosures are very small, and typically have a history of being previously grazed by livestock before the exclosure was constructed, studies of truly ungrazed plant communities are limited to a handful of relict areas where livestock have been continuously excluded (Fleischner 1994). Small exclosures do not include a wide variety of soils, slopes, and aspects, and can be heavily grazed by rodents (Gardner 1950).

Manier and Hobbs (2007) review the literature on effects of ungulate exclosures. Unburned exclosure areas had twice as much leaf litter (Davies et al. 2009). Exclosures had the greatest proportion of long-lived perennial grasses, the greatest soil stability, the least potential for erosion, and showed the least ecosystem degradation (De Soyza et al. 2008). In the Mojave Desert, grazing exclosures were characterized by greater biomass of native vegetation, and greater diversity of rodent species (Brooks 1995). The herbaceous understories of salt desert scrub communities are readily eliminated by overgrazing, but exclosures present for 11 years resulted in remarkable recoveries of native grasses (Billings 1949). Duniway et al. (2018) found that the effects of grazing exclusion on salt desert soils of the Colorado Plateau varied by soil type. After 50 years of exclusion, perennial grasses increased significantly on some exclosure soils, and cheatgrass decreased significantly in exclosures on some soil types, while the grazed areas continued to show deterioration of range condition and high levels of soil erosion and compaction, even with the lower stocking rates in comparison to stocking rates prevalent at the time when the exclosures were created. Cheatgrass occurred more frequently in salt desert scrub that was grazed than in grazing exclosures in a study by Turner (1971). In Wyoming, Muscha et al. (2004) found mixed results on whether exclosures showed restoration of native vegetation after exclusion of cattle for 30-45 years. Muscha et al. (2004) measured exclosures that were often far from roads and had limited compositional changes from inside and outside these exclosures. Robertson (1971) found a marked recovery of grasses and forbs over 30 years of livestock exclusion in Nevada, but cheatgrass was not a significant component of the exclosure, either at the onset or after livestock exclusion. Ponzetti and McCune (2001) examined Oregon exclosures ranging in age from 11 to 59 years, and found slightly more perennial bunchgrasses inside the exclosures, but not significantly so. Rangeland conditions in another study showed that the grazed treatments were significantly worse than in the exclosure (Willms et al. 1990). Yeo (2005) found that grazing exclosures increased soil crust and perennial bunchgrass regeneration, which was suppressed by moderate grazing in surrounding areas. In this study, about half of the sites with exclosures (ranging in age of emplacement from 18 to 38 years) moved significantly toward ecologically pristine conditions, while exclosures on a few sites showed no progress. In contrast, on the Northern Plains, Vermeire et al. (2018) found that grazed pastures and livestock exclosures had similar productivity, but grazed pastures had greater diversity and species richness for plants. In California, exotic annuals dominated grazed areas, while native grasses were of coequal dominance with invaders in fenced grazing exclosures (HilleRisLambers et al. 2010). Davies et al. (2010) found that lands subjected to moderate levels of grazing had half the standing crop of herbaceous vegetation than exclosures protected from grazing for 70 years, and hypothesized that the ungrazed exclosures were therefore at a greater risk for fire. However, 15 years of exclosure had little effect on the response of Northern Plains grasslands to fire (Vermeire et al. 2018). When livestock were excluded for seven years, plant diversity inside exclosures was lower, and cheatgrass increased slightly (Loeser et al. 2007). Exclosures at more arid sites showed little response to livestock removal, while exclusion of livestock resulted in greater recovery at mesic sites (Muscha et al. 2004). Exclusion of grazing by all large herbivores (including wildlife) reduced plant diversity (Manier and Hobbs 2007).

In one study, montane voles and cottontail rabbits became the primary grazers in the absence of livestock, but these rarely caused the death of cheatgrass seedlings (up to 6.4% of a seedling cohort) (Mack and Pyke 1984). Anecdotally, grasshoppers and Mormon crickets feed preferentially on perennial grasses over cheatgrass, as do jackrabbits (Stewart and Hull 1949). Grasshopper herbivory on cheatgrass is ineffective at restricting the population growth of cheatgrass (Beckstead and Augspurger 2004). In the absence of livestock grazing, lagomorphs can suppress the recovery of native bunchgrasses when their numbers are high (Stewart and Hull 1949, Knapp 1996).

Grazing exclosures have been found to have low levels of cheatgrass (Laycock 1967). On the Northern Plains, Vermeire et al. (2018) found that cheatgrass was six times as abundant in grazed pastures as inside exclosures during two out of three years. Muscha et al. (2004) found cheatgrass greater inside exclosures at some sites, and outside exclosures in others. In Nevada, cheatgrass cover was not significantly different inside grazing exclosures almost 70 years old when compared to outside exclosures (Courtois et al. 2004). In west-central Utah, Kitchen and Hall (1996) found that ungrazed exclosures had more perennial bunchgrass and shrubs of shorter stature. Exclosures had more C_3 grasses and fewer C_4 grasses than either lightly (20%) or heavily (60%) grazed pastures for shortgrass prairie; soil carbon cycling rates were similar across treatments (LeCain et al. 2002). In Nevada, shrubs showed significantly greater cover inside exclosures than outside exclosures (Courtois et al. 2004). In Colorado sagebrush habitats, Manier and Hobbs (2007) found that excluding grazing resulted in threefold greater shrub cover and less bare ground.

According to Stewart and Young (1939), perennial grass competes more strongly with cheatgrass when it has not been overgrazed. Warg (1938: 22) postulated, "findings on all overgrazed lands indicate that, with complete protection and provided the rootstalks are not entirely destroyed, bunchgrasses as a rule will come back and assume their place in grassland types in a relatively short time." Anderson and Inouye (2001) found that increases in plant species diversity and heterogeneity from 1950 to 1975 at the Idaho National Laboratory were largely attributable to recovery of vegetation from drought and livestock grazing.

Sandberg's bluegrass, squirreltail, needle-and-threadgrass, and streambank wheatgrass have been known to invade cheatgrass stands, converting invaded areas to perennial cover (Monsen 1994). Arredondo et al. (1998) also reported that squirreltail is known to invade cheatgrass monocultures. Mata-González et al. (2007) modeled cheatgrass and perennial grass dynamics based on data from the U.S. Army Yakima Training Center in eastern Washington and found that in the absence of livestock grazing and military training disturbances, cheatgrass dominated both burned and unburned plant communities, after which annuals were replaced by perennial grasses over time. Early-seral old-field succession on the Southern Plains was dominated by annual forbs, mid-seral succession was dominated by cheatgrass, which was then replaced by perennial grasses and forbs (Paschke et al. 2000).

Cheatgrass commonly occurs as a minor component in healthy native bunchgrass communities (Klemmedson and Smith 1964). Cheatgrass can persist in competition with little-disturbed native vegetation in small stands (Hulbert 1955). Belnap and Phillips (2001) found that when cheatgrass initially invades ungrazed areas, it does not have a measurable impact on native bunchgrass cover but does have a significant effect on soil biota and processes. Kindschy (1992) documented cheatgrass colonization of kipukas in the midst of old lava flows that have never been grazed by livestock, but cheatgrass remained a minor component of the vegetation and the cover of native plant species remained unaffected. Stewart and Young (1939) found that cheatgrass colonized several areas supporting a vigorous growth of native perennials but did not become dense.

The overwhelming body of science reviewed above shows that long-term grazing has contributed to major increases in cheatgrass cover. However, a few researchers have suggested that cessation of livestock grazing can increase cheatgrass. Knapp (1996) hypothesized that deferral of grazing increases cheatgrass biomass, because native perennials have been suppressed and their seeds are scarce in the seedbank. Davies et al. (2009) found that areas left ungrazed for more than 65 years increased their cheatgrass cover after burning eightfold more than lands grazed at 30-40% utilization (an unusually light level of grazing in the arid West), when burned and left ungrazed for 14 years. Cheatgrass infestations can remain heavy even 24 years after cattle are removed (Sperry et al. 2006). In California annual grasslands on serpentine soils, cessation of livestock grazing enhanced the dominance of non-native annual grasses (Hobbs and Huenneke 1992). Young and Allen (1997) asserted that once cheatgrass reaches an equilibrium condition, the idea that removal of grazing eliminates cheatgrass is false. Vallentine and Stevens (1994: 205) asserted that rest from grazing was hopeless unless a significant amount of native vegetation remains.

However, with sufficient time and in the absence of livestock grazing, cheatgrass will ultimately be replaced by native vegetation. The length of time required varies greatly, depending on local conditions. Rice and Westoby (1978) found that after 15 years of exclusion of jackrabbit and/or domestic sheep, cheatgrass density increased in some habitat types, and decreased in others. One Utah population of montane cheatgrass in the Nebo Pass area studied by Ramakrishnan et al. (2006) ultimately became extirpated due to succession to perennial vegetation (Arnesen et al. 2017). McLean and Tisdale (1971) estimated that it takes 20 to 40 years in fescue grasslands and ponderosa pine woodlands for overgrazed rangelands to return to excellent condition. In an eleven-year study in central Utah, Hosten and West (1994) found that cheatgrass densities fluctuated from year to year, starting with a high density in the early years of the study and ending with negligible cheatgrass presence by year 10. Lavin et al. (2013: 1639) predicted that native species restoration efforts in Wyoming big sagebrush steppe would require long periods of stability and lack of physical disturbance, or else they risk failure. Young et al. (1987) predicted that the natural return of perennial grasses on burned, degraded sites in the Great Basin could well exceed a century, even with the exclusion of livestock grazing.

Stewart and Hull (1949) considered cheatgrass an intermediate successional plant that would be replaced with perennial forbs and grasses over time. Garner et al. (2019) added that native species may take many years to increase from low densities following the removal of landscape disturbances such as grazing, due to seed limitation or seedling recruitment issues. In eastern Colorado, annual grass cover (almost entirely *B. tectorum*) increased to 39% seven years after Conservation Reserve Program fields were fallowed, then declined to almost no cover after 18 years (Munson and Lauenroth 2011). In southern Idaho, Rice and Westoby (1978) found relatively slight recovery after 15 years of excluding both domestic sheep and jackrabbits.

Little change in plant composition occurred in the first 10 years following exclosure construction (McLean and Tisdale 1971). In two long-term livestock exclosures in the Magic Valley of Idaho, one is returning to native bunchgrasses after 50 years (although cheatgrass remains a significant component), while the other remains dominated by cheatgrass (Hironaka 1986). At INL, it took about 30 years for perennial grasses to increase significantly after the cessation of livestock grazing (Anderson and Inouye 2001). After 30 years of protection from grazing, a New Mexico tract showed significant increase in grass cover, but still had a long way to go to reach full recovery (Gardner 1950). Hironaka and Tisdale (1963) reported that squirreltail (*Elymus spp.*) can ultimately replace cheatgrass over a period of 23 years. Warg (1938) demonstrated the return of bunchgrasses in cheatgrass-infested plowed fields after 7-10 years, with faster recovery (as little as two years) on cheatgrass infestations on overgrazed rangeland rested from livestock. Driscoll (1964) documented cheatgrass at 1.7% cover on a juniper woodland rested from livestock grazing for 35 years. Almost forty years later, cheatgrass cover was down to 0.1% on the same site (Fox and Eddleman 2003). However, despite the cessation of cattle grazing at the Hanford Nuclear Reservation in central Washington, cheatgrass continued to make up 15 to 22 percent canopy cover thirty years later, making it the most abundant herbaceous species (Cline et al. 1977). These researchers characterized it as "so well adapted to the climactic and soil conditions of the Hanford Reservation that it is prudent to consider the species as an integral part of the flora," and they recommended using cheatgrass for revegetating disturbed lands (Cline et al. 1977: 68). It may take more than 50 years of rest from livestock grazing to recover arid areas to a natural state, and this slow recovery is particularly attributable to the slow pace of biological soil crust recovery (Duniway et al. 2018).

Preventative Measures

The exclusion of invasive plants before they invade, or at least early detection and rapid response, are the most cost-effective and successful ways to prevent the negative ecological and economic impacts of cheatgrass infestations (Brooks et al. 2004, 2008). Once perennial bunchgrasses have been substantially replaced by cheatgrass, a threshold has been crossed and restoration to native vegetation becomes difficult and expensive (Eiswerth et al. 2009, Davies et al.

2012a). Billings (1990) asserted that it is not possible to remove or control cheatgrass once it has become dominant, he suggested the best approach is to prevent further expansion of cheatgrass from its present distribution. According to Garner et al. (2019: 94), prevention is more economically efficient than removal or other control efforts once an infestation has occurred. Because restoration of cheatgrass-invaded sagebrush habitats is so difficult and expensive, prevention of invasion must play an important role (Davies et al. 2011a).

In resilient landscapes, fire does not promote the spread of cheatgrass. Cheatgrass cover decreased with increasing time since fire, while native bunchgrass cover increased with fire and with time since fire (Condon and Pyke 2018). According to Brooks and Chambers (2011), land managers should focus on reducing fire and overgrazing, reducing disturbance and corridors for infestation, and greater detection efforts to control cheatgrass. Managing for sufficient density and cover of native perennial grasses and forbs and biological soil crusts to prevent the establishment or population growth of the invader is generally the most successful tool for maintaining resistance to plant invasions (Chambers et al. 2014, Garner et al. 2019).

Meyer (2011) recommended that land managers should manage for intact shrubland communities capable of rebounding from disturbances such as prolonged drought and fire without high risk of cheatgrass dominance. Lockyer et al. (2015) found that protecting areas within intact sagebrush ecosystems with increased shrub canopy cover (greater than 40%) and perennial grasses should improve the reproductive success of sage-grouse. They also suggest that reducing the further spread of cheatgrass should protect sage-grouse nesting habitat currently on the landscape. Coates et al. (2015) called for protecting low reliance and resistance habitats of conservation importance from fire and enhancing resilience and resistance in moderate and high resilience and resistance habitats in the early stages of cheatgrass invasion. Suring et al. (2005) argued for focusing prevention and control efforts on lands at moderate risk of displacement by cheatgrass, on the basis that it is too late to save areas with high risk.

Ultimately, cost savings by preventing cheatgrass invasion could easily eclipse the relatively manageable economic consequences of livestock reductions. Brooks (2008a: 44) concluded, "There may be economic costs associated with exclusion of plant species that are used in ornamental horticulture or as livestock forage, but these short-term costs would be eclipsed by the long-term costs of inaction" if the invasive species becomes established.

CONCLUSIONS AND RECOMMENDATIONS

Cheatgrass is one of the most significant ecological crises facing land managers in the arid West. Its expansion is caused by heavy livestock grazing that degrades or eliminates the biological soil crusts and native grasses that are the best natural defense against weed invasion. Once established, cheatgrass promotes unnaturally large and frequent fires that cement its dominance as a weed monoculture of little value to either livestock or native wildlife. Cheatgrass invasions impoverish native ecosystems and degrade or even eliminate habitat function for native animals, exacerbating the biodiversity crisis. As cheatgrass increases, it fuels larger and more frequent fires that eliminate shrub cover, further stress native grasses, and contribute to increasing levels of cheatgrass dominance. Cheatgrass invasions can be expected to expand further as climate places native plant communities under further stress and creates climactic and atmospheric conditions more favorable to cheatgrass than to native vegetation. The expansion of cheatgrass exacerbates the climate crisis itself by converting native grasslands and shrublands with high rates of carbon storage to annual grasslands that burn frequently and through fire and decomposition are net emitters of carbon into the atmosphere. Minimizing and restoring cheatgrass infestations should therefore be a priority dictating the outcomes of land-use and land management decisions throughout the arid West.

Based on this review of the scientific literature, we offer the following recommendations for preventing further cheatgrass expansion and dominance, and for rehabilitating areas where cheatgrass invasions presently occur:

- For lands where cheatgrass remains a minor component of the overall vegetation, and native grasses remain abundant, limit livestock grazing at or below 30% forage removal to prevent soil disturbance and stress to native perennial grasses.

- For lands where cheatgrass is dominant over large areas, completely remove livestock, for a sufficient period of time (spanning decades or even a century or more) to allow native vegetation to naturally re-establish. It may be necessary to close and restore the area to perennial plants.

- Public lands not meeting land health standards for livestock-related reasons should be closed and rested from livestock grazing until recovery of native plant species and biological soil crusts is achieved. Manage public lands for the benefit of biological soil crusts.

- For lands where severe cheatgrass infestations are quite small (a few acres or less), treat with a combination of herbicides, natural pathogens, and seeding with native grasses and shrubs (preferably seeds or seedlings from a geography as close as possible to the site being treated). These lands should be rested from livestock grazing until native plants are sufficiently established to prevent cheatgrass from re-establishing dominance.

- Limit livestock grazing on public lands to the winter dormant season where possible, and avoid spring and summer grazing. Initiate fall grazing only after soil moisture is established by fall rains, to decrease soil disturbance.

- Quarantine livestock that have grazed in cheatgrass-infested areas for at least 3 days, and longer in muddy conditions, before moving them to new areas, to reduce seed transfer.

- Re-seed with native species of plants and severely limit seeding with non-native grasses, forbs, or shrubs – during post-fire or post-disturbance rehabilitation – to prevent creating a new invasive weed problem to replace the original one.

- Do not apply targeted grazing over large acres unless and until rigorous methodologies can be developed and applied that reliably return invaded areas to native plant communities.

- Prevent pinyon-juniper removal in areas where woodlands are mature and/or lack herbaceous/shrub understories, and in areas where cheatgrass invasion is dominant. In areas where pinyon/juniper expansion is in the early stages and a healthy understory of native grasses and shrubs is present (and cheatgrass is minimal to absent), limit tree removal to hand-cutting to preclude disturbance by heavy machinery that encourages cheatgrass invasion of treated lands.

- Avoid soil disturbance that creates a seedbed for cheatgrass. Minimize use of bulldozers or other ground disturbing equipment when establishing fire lines for wildfires. For prescribed fires, do not use fire lines made by heavy ground-disturbing equipment.

- Limit vehicle access to roads and trails designated as open, and close areas to off-highway vehicular use.

- List cheatgrass as a noxious weed at federal, state, and local levels. Require that hay be certified weed-free in regard to cheatgrass, to prevent spread, and genetic mixing of populations. Require a quarantine period for livestock foraging in cheatgrass-infested areas before they are transported to areas where cheatgrass does not occur at problematic levels.

The key to combating weed invasions is to prevent the types of conditions and land uses that confer advantages to weed species over native plants, and to restore native plant associations that are resilient and resistant to future weed invasion. Once cheatgrass reaches critical thresholds (achieving 5% or more in surface cover on low-resilience habitats or 25% cover in high-resilience habitats, Garner et al. 2019), it becomes difficult to control. Garner et al. (2019) state that through excessive livestock grazing or other human-caused disturbance, a positive-feedback cycle becomes entrenched that moves inexorably toward a cheatgrass monoculture, destroying native plant communities. A preventative approach is imperative to avoid further expansion of cheatgrass. The costs and difficulties of combating both further cheatgrass expansion or retention – and minimizing the frequent fires that result – are high from both the ecological and the economic perspectives.

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