RESTORING SEMI-ARID LANDS

WITH MICROTOPOGRAPHY

by

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DEDICATION

I dedicate this work to my sisters, Ashley and Lauren, the reasons my sky is so sunful. Thank you for your support now and always.

i am so glad and very
merely my fourth will cure
the laziest self of weary
the hugest sea of shore

so far your nearness reaches
a lucky fifth of you
turns people into eachs
and cowards into grow

our can'ts were born to happen
our mosts have died in more
our twentieth will open
wide a wide open door

we are both and oneful
night cannot be so sky
sky cannot be so sunful
i am through you so i

-#49, E.E. Cummings

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ABSTRACT

Water is often limiting to plant establishment in semi-arid lands, and this limitation can be especially pronounced in restoration contexts where human legacy impacts and/or non-native plants are present. The application of herbicide and mulch can help retain soil moisture by killing unwanted plant species or lowering evaporative losses, respectively. Creation of microtopography, or soil surface variation, is a third technique that could alleviate growing-season water shortages. Here we report findings from a study that explored the effects of these three techniques combined with broadcast seeding a mix of four native grasses, one native shrub, and one native forb for increasing plant canopy cover and density at three sites in northern Yellowstone National Park. One year after treatment, plant cover in control plots averaged 60%. Across plots treated singly with 1.5% glyphosate herbicide, 3 cm of red cedar mulch, or hand-dug microtopography, only mulch and microtopography increased canopy cover relative to control plots, although the increase consisted mostly of non-native species (>97%). Herbicide, not surprisingly, decreased canopy cover, and that decrease also consisted mostly of non-native species. The herbicide treatment was the most effective in encouraging native species canopy cover and density while simultaneously reducing the same measures of non-native species. Microtopography treatments encouraged growth of all plants (native and non-native), particularly in the micro-lows, but for this to be an effective restoration strategy, non-native species must first be controlled. Although herbicide was quite effective at reducing non-native species populations, particularly at the Cinnabar site, spraying must be timed with the phenology of the existing non-native plant community. We learned that reducing competition with non-native plants does not necessarily encourage native plant growth, which may indicate that growing conditions need to be improved at this site before restoration can be successful. Taken together, our results suggest that soil amendments like microtopography and mulch may have beneficial restoration applications in semi-arid lands but may also show little benefit on a short time-scale in a highly disturbed system. Areas plagued by non-native species invasions and legacy agricultural and grazing impacts are likely to require careful planning of restoration approaches in order to claim long-term success.

CHAPTER ONE

LITERATURE REVIEW

Restoration in Semi-Arid Lands

This chapter explores ways to restore impaired ecosystems, focusing on physical, chemical, and biological techniques. Many degraded areas, especially in semi-arid regions of the world, need one or a combination of restoration techniques to prevent non-native species from complicating restoration efforts. Non-native species invasions can be explained in part by vacant niches within a plant community or by other factors such as propagule pressure, invasive traits, and the invasibility of the novel environment. The history of a restoration site can also influence restoration success. Evolution, glacial history, and past human impacts can all contribute to the success or the failure of a restoration project in the long term. These topics are discussed in detail below.

In 1956 the world's leading ecologists detailed anthropogenic changes to ecosystems in every corner of the globe, including deforestation, conversion of forest to agricultural land, and fire suppression (Curtis, 1956). In the 50 years following, humans more rapidly and intensely degraded ecosystems than during any other 50-year period in history (Safriel & Adeel, 2005). Out of recognition of such severe degradation arose the field of restoration ecology, which emphasizes preserving species biodiversity, building ecosystem resilience, and striking a balance between nature and culture (Hall, 2005; Jordan & Lubick, 2011; Society for Ecological Restoration, n.d.). The discipline of restoration ecology accounts for human uses and interactions with the environment; it recognizes the importance of restoring ecosystem functions like nutrient cycling and net primary production, which can improve ecosystem services like food production and clean drinking water (Kleindl et al., 2018). The need for restoration is widespread (Gibbs & Salmon, 2015), but our changing climate as well as additional interacting threats (*e.g.*., ocean acidification, desertification, eutrophication) could limit our ability to restore ecosystem structure and function (Harris et al., 2006).

We must look beyond traditional restoration practices to accommodate future shifts in climate and climate variability. The global land surface, for example, is increasing in aridity due to changing climatic patterns (Huang et al., 2015; Salem, 1989). As of 2000, the Millennium Ecosystem Assessment determined about 15% of Earth's terrestrial surface was considered semi-arid and 15% of the world's population live in these areas (Safriel & Adeel, 2005).

Semi-arid ecosystems are defined as having an aridity index (AI_U) of 0.2 to 0.5 and a Bailey Moisture Index (S) of 2.5- 4.7. AI_U is defined as:

$$AI_U = \frac{P}{PET}$$

where P is average annual precipitation and PET is potential evapotranspiration (United Nations Environment Programme, 1992). S is defined as:

$$S = \sum_{i=1}^{12} s_i$$

where the monthly moisture index s_i is 0.18 $p/1.045^t$, which considers both mean monthly precipitation in cm (p) and mean monthly temperature (t) in °C (Hall et al., 1979). Both these indices are indicators of semi-arid environments. With the threat of more frequent and intense droughts in semi-arid regions (Dai, 2012; Whitlock et al., 2017), restorationists interested in ecosystem services provided by semi-arid zones, whether those services are obtained directly or indirectly, may be forced to innovate restoration techniques that anticipate increasing aridity.

Studies in semi-arid lands have shown that water uptake drives plant distributions as different vegetation types compete for water (Blumler et al., 1993; Eagleson & Segarra, 1985; Walker & Noy-Meir, 1982). Once established, plants in semi-arid regions have mechanisms to survive seasonal drought (Chaves et al., 2003), but seeds in these regions typically are adapted to germinating in the spring or fall when moisture availability is higher. These same plants therefore may be sensitive to moisture stress if aridity were to increase or if spring or fall soil moisture were to fall below average (Baskin & Baskin, 1998), which could limit restoration success. Dryland restoration strategies that reduce a re-establishing plant community's dependence on precipitation patterns (*i.e.*, amount and frequency) could improve the odds of long-term restoration success. Next, we review physical, chemical, and biological approaches to restoration. These three approaches to restoration are specific in this study to improving local environmental soil conditions in harsh, semi-arid restoration areas and to controlling non-native species. Each of the restoration approaches will address both environmental soil conditions and non-native species, although not every restoration technique can address both of these issues.

Physical Approaches to Restoration

Physical restoration approaches include, but are not limited to, the use of fire and mechanical tillage to control non-native species or the use of microtopography or mulch to alter soil water conditions.

Fire

In areas with non-native plants, low-intensity, infrequent prescribed burning can reduce the fraction of non-native seed in the seed bank by killing live seeds on plants (Hamilton, 2014). In order to reduce non-native propagule pressure, burning can be timed to coincide with standing dead plants or live plants that have gone to seed. In some cases, burning can increase mineralized nutrients available in the soil, thereby improving environmental conditions for restoration. In other cases, burning can decrease nutrients from the system by volatilization or smoke release (Woodmansee & Wallach, 1981), producing undesirable soil conditions for establishing new plants on a restoration site. Other negative results include decreased soil organic matter, lower total nitrogen in the soil, altered carbon allocations in plants, a change in species composition and succession, and altered rates of evapotranspiration (Biederback et al., 1980; Blair, 1997; Daubenmire, 1968; Ojima et al., 1994; Towne & Owensby, 1984). The outcomes of burning in a restoration context therefore depend on a suite of factors such as time of year, frequency, intensity, and duration of the fire, as well as the amount of plant aboveground biomass and leaf litter. Burn treatments must be carefully planned to avoid further degradation of an invaded habitat.

Tillage

Tillage is common in agronomic systems, but it is not often recommended as a restoration practice in natural areas. Natural areas have a suite of factors that make tillage unpractical including terrain, soil type, existing vegetation or rocks, and remoteness of the area. Agronomic systems that are easily accessible for equipment use tillage to prepare the soil for seeded species while reducing the presence of non-seeded species; fields are often tilled multiple times for consecutive growing seasons to first stimulate undesirable seed germination, and then again to mechanically kill those small seedlings. This practice may be continued until the seed bank is depleted. Evidence for this strategy shows inconsistent results or suggests that tillage may actually promote non-native species by reducing compaction (Page Kyle et al., 2007; Tuesca et al. 2001). Other studies show non-native species decrease when tilled, especially in combination with other control methods like herbicides (Miller & D'Auria 2011). Tillage is sometimes recommended as a method for reducing non-native species populations (Sheley et al., 2011; U.S. Department of the Interior Fish and Wildlife Service, 2009), but no-till systems have risen in popularity due to soil health considerations.

Microtopography

Creation of microtopography is a dryland restoration strategy that may lessen the deleterious impacts of aridity on re-establishing plant species by increasing soil water availability. Microtopography is defined as naturally occurring or human-constructed soil surface roughness, consisting of convex micro-highs and concave micro-lows (Kishné et al., 2014). Microtopography can exist on many scales; for example, at the landscape level, microtopography at the kilometer scale can affect species richness (Ruifrok et al., 2014). Millimeter-scale microtopography, on the other hand, may expose a remnant, recalcitrant seed bank during microtopographic installation, encouraging dormant seeds to germinate (Templeton & Levin, 1979). The focus here is on decimeter-scale microtopography as a restoration strategy for encouraging individual native plant establishment. More specifically, there are three direct or indirect water-related benefits of microtopography: storage of rain or snow in micro-lows (Figure 1 [images sourced from the Noun Project, Condiff; Lloyd]), retention of windblown organic material, and protection from wind and/or desiccation as an advantageous "nurse site" for germination and establishment of target plants.

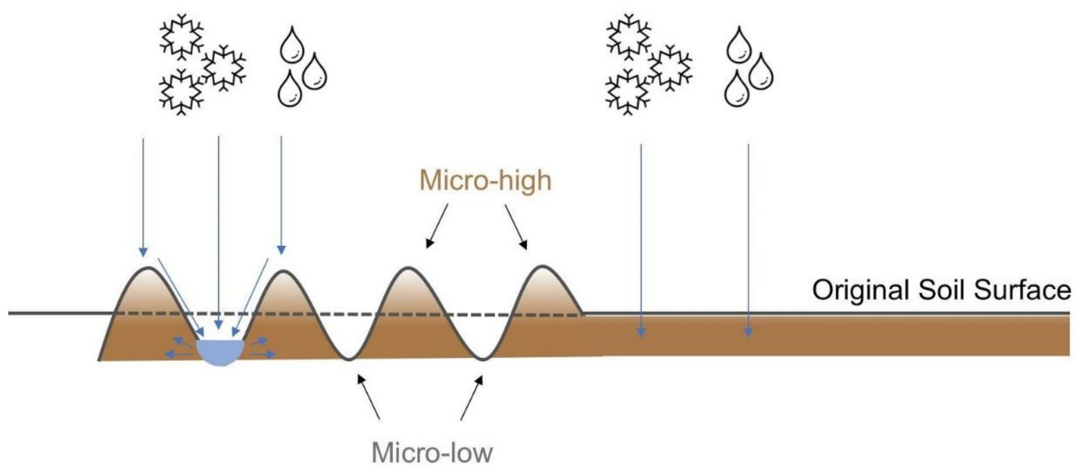


Figure 1. Manipulation of the original soil surface leads to microtopographic variations that can redistribute and concentrate precipitation into micro-lows.

<u>Precipitation Storage.</u> Microtopography modifies local hydrologic patterns by enabling precipitation to collect in micro-lows (Figure 1). Micro-lows, with their bowl-like shapes, can store a larger volume of water than surrounding micro-highs or unmanipulated areas (Appendix A, Figure A1; DOI: 10.5281/zenodo.1213337). This can

increase the depth to which water infiltrates into soil (Dunne et al., 1991). A simplified model of microtopography implemented on a hillside showed soil water infiltration depths increased between 20% and 200% compared to a hillside lacking microtopography (Thompson et al., 2010). Even small increases in runoff slope length (*i.e.*, from micro-highs to micro-lows on the decimeter scale) can increase the depth of infiltration (Fox et al., 1998). In the winter and early spring months, micro-lows may also create a colder, wetter microclimate by accumulating a deeper snowpack or retaining ice further into the growing season (Bennie et al., 2008; Dillard, pers. obs.; Appendix A, Figure A1; DOI: 10.5281/zenodo.1213337). In doing so, micro-lows can locally maximize the volume of retained snowmelt, which could increase soil water infiltration by concentrating precipitation, but which could also lower infiltration as the soil could remain saturated or frozen longer than adjacent micro-highs. A deeper and later snowpack held in the micro-lows could also delay the localized timing of snowmelt to coincide more with summer annual or perennial plant growth demand than with winter annual plant growth demand.

<u>Catchment Basins.</u> Micro-low surfaces are depressed from the surrounding landscape, and therefore, are able to catch materials transported by water and wind. In addition to trapping water and locally eroded soil, micro-lows can accumulate windblown aeolian dust, organic matter, and seeds. Aeolian dust can aid restoration success with its high specific surface area and associated ability to retain water and provide nutrients (Belnap, 2003). Soil organic matter, which is typically concentrated in the upper few centimeters of the soil, also has very high specific surface area and can store vast

quantities of plant-available water and mineralizable nutrients compared to mineral-dominated soil components (Brady & Weil, 2010). Seeds that collect in micro-lows from nearby ecosystems may help diversify and rejuvenate the existing seed bank, although this seed rain could also contribute undesirable, non-native species.

The effects of microtopography depend on the scale by which it is implemented. On a landscape scale, micro-lows can trap water, soil, and biomass via overland flow from higher elevations. Multi-meter-scale (bulldozer-sized) microtopography was used at a severely contaminated mine-affected site in Anaconda, MT, to control erosion and sediment transport and to help retain surface water (Montana Department of Justice, 2007).On a centimeter- or decimeter-scale, the material collected in micro-lows is transported from adjacent micro-highs, and is likely to be a smaller volume and diversity of material (Kishné et al., 2014).

<u>Nurse Sites.</u> A meta-analysis of nurse plant benefits showed that seeds growing underneath shrubs, which are perhaps similar growing conditions to the micro-lows of plant wells, were physically protected and had greater access to water and nutrient stores compared to seeds growing in unmanipulated areas (Flores & Jurado, 2003). Here, I hypothesize that micro-lows created by microtopography can act as “nurse sites,” having similar effects to nurse plants, but instead of directly providing water and nutrients, nurse sites provide shelter. Shelter may protect seeds and emerging plants against wind disturbance. For example, seeds in micro-lows may be protected from wind displacement, and emerging plants sheltered against disfiguration from wind disturbance. Restoration using wind barriers (“ConMods”) in an arid region in southeastern Utah resulted in a 10-

fold increase in probability of native species presence relative to control areas, as the wind barriers acted as nurse sites for emerging seeded species; wind barriers first accumulated wind-blown biomass, which then provided increased protection from solar insolation and desiccation (Fick et al., 2016). Nurse sites may provide shelter against wind and sun, which can be harsh and relentless to seedlings in semi-arid regions.

Another idea in creating a nurse site is first seeding it with a cover crop. Sparsely planted cereal grains with low competitive ability can be used as “nurse crops” in restoration settings, which may bolster perennial grass establishment, and even change successional patterns (Whisenant, 2002). Semi-arid restoration projects can depend on initial seedling survival, although few studies have quantified methods for protecting seedling against harsh environmental conditions.

Mulch

Surface mulching is another strategy that may aid restoration success in dryland restoration contexts. In agronomic settings, mulch has been shown to increase crop yields (Jones Jr. et al., 1969). Mulch in semi-arid regions has been used to maintain soil water by reducing water lost to evaporation (Groenevelt et al., 1989; Ji & Unger, 2001). As a result of reducing evaporative losses, a surface layer of mulch may lengthen the amount of time necessary for soil to fully desiccate to its wilting point, both changing the amount of water and the timing of water available to plants (Bond & Willis, 1969). Microbial activity, which strongly tracks soil moisture patterns, increases under surface mulching (Tiquia et al., 2002). Increased microbial activity, in turn, could accelerate organic matter mineralization rates, improving nutrient availability (Brady & Weil, 2010). Conversely, the high carbon-to-nitrogen ratio of woody mulch amendments can depress plant-available-nitrogen as microbial demand increases (Brady & Weil, 2010). Mulch can also slow microbial processes, which generally decrease with decreased temperatures and saturation, if the soil beneath the mulch stays colder and wetter in the spring and/or early summer.

It's important to note that there are many different types of mulch and many ways to use it. Woody mulches may be used to form physical barriers between the soil surface and the atmosphere because they are hardy and likely to stay in place without too much disturbance. They may also raise the C:N ratio though, which could be undesirable in nutrient-limited settings. Straw mulches may lower the C:N ratio but may blow away in areas of moderate to high winds. Characteristics of individual mulch materials should be carefully considered and should be appropriate to the goals of the restoration project. Mulch should be sourced locally whenever possible for restoration projects to avoid introducing weeds or pathogens and to provide cover appropriate to habitat type (*i.e.,* cedar bark mulch for a forested restoration site).

Chemical Approaches to Restoration

This section will address only herbicide as a chemical approach to restoration. Of course, there are techniques other than herbicides that might be useful in other restoration contexts, but here we focus on non-native plant control. Techniques like liming or fertilizing may be appropriate in other studies, but this study did not require, or in some cases, permit other chemical methods.

Herbicide

Large-scale restoration projects might command the broad-scale use of herbicides if non-native species are a problem. Non-discriminatory, post-emergent herbicides systematically kill all germinated plants, although selective herbicides might be favored in restoration settings for their targeted effects. Selective herbicides such as broadleaf herbicides, for example, kill forbs without negatively impacting graminoids. Selective herbicides can help restorationists target undesirable vegetation while minimizing the damage to desirable plants, depending on the stage of restoration. Additional options for herbicides include pre-emergent herbicides, which target the germinating seed bank but not established plants. Some herbicides have residual effects in the soil, which delays the timing of planting, as planting should not occur if traces of herbicide remain in the soil. Some high-residual herbicides can persist, active or inactive, in the soil for months or even years following application (Colquhoun, 2006), and planting needs to be coordinated with the specific chemical used. Areas sprayed with herbicides without residual effects (*i.e.*, glyphosate) can be planted almost immediately after an application.

Biological Approaches to Restoration

Biological approaches to restoration use a living organism to control vegetation. Examples include, but are not limited to, insects, plant pathogens, or grazing to target specific plants. Here we focus on grazing by domestic livestock as a restoration technique that can be applied at a large scale without risk of impacting nearby lands.

<u>Grazing</u>

Wild grazers such as elk (*Cervus canadensis*) and bison (*Bison bison*) are not used as targeted restoration tools because their behaviors are not controlled like those of domestic grazers. In areas of high grazer densities (both natural areas and farmed lands), vegetation can suffer (Hebblewhite et al. 2006; Knapp et al., 1999). Hoof action and subsequent compaction can biologically alter soils by reducing the available pore space for soil biota and gas exchange (Greenwood & McKenzie, 2001). Reducing pore space, and with that, the presence of soil macropores, can decrease water infiltration rates and soil water holding capacity (Greenwood & McKenzie, 2001). While compaction could be helpful in reducing non-native plant populations (Page Kyle et al. 2007), it could be detrimental for establishing native plants, and sometimes actually encourages non-native plant populations which tend to capitalize on areas of high disturbance (Gurevitch & Padilla, 2004; Didham et al., 2005). Fencing a restoration project is one strategy to exclude grazers from established grazing lawns for several growing seasons while native plants are establishing. The sizeable cost of fencing (*e.g.*, ~ $10-13 per linear foot; Renkin, 2014) or the area of the restoration project may limit the feasibility of grazer exclusion in restoration projects, especially in natural areas with high wild grazing populations. In areas with high grazing pressure, however, excluding grazing animals may be necessary to reestablish a high-biomass native plant community (Gonzales & Clements, 2010).

In some mature restored ecosystems where grazing is a keystone process (*i.e.,* grasslands), wild grazers may be re-introduced to the system, but only after successful native plant establishment. Even then, grazer populations must be appropriate to the size of the restoration area and to the stage of the restoration project.

In addition, wild animals preferentially graze according to season and diet. For example, bison repeatedly return to the same “grazing lawns” and even the same individual grass plants over the course of a season, almost completely ignoring forbs and shrubs (Knapp et al., 1999).

Targeted grazing with domesticated animals such as cattle (*Bos taurus*), sheep (*Ovis aries*), or goats (*Capra aegagrus hircus*) is more controlled but is not without risks. Grazing must be carefully planned and timed to ensure grazers are reducing populations of non-toxic and undesirable plants without decimating native plants populations or harming the soil conditions of the restoration site. Caution must be exercised, as many non-native plants common to the western United States are toxic to grazers (*Cynoglossum officinale* [Houndstongue], *Halogeton glomeratus* [saltlover], *Kochia scoparia* [burningbush], *Solanum nigrum* [black nightshade], *Hypericum perforatum* [common St. Johnswort], *Melilotus alba* [white sweetclover], *M. officinalis* [yellow sweetclover], *Senecio jacobaea* [stinking willie], *Centaurea solstitialis* [yellow star-thistle], *C. repens* [Russian knapweed], and others). Because these species are seldomly grazed, animals grazing an area dominated by any one or combination of these toxic plants will preferentially eat other plants at the restoration site. The lack of herbivory may give toxic, non-native plants a competitive advantage over native plants which are more consistently grazed over the course of a growing season. In degraded areas or under stress conditions like overgrazing or wildfire, poisonous plants are sometimes consumed, in some cases leading to grazer injury or death (Panter et al., 2011).

To further complicate targeted grazing, grazers have been observed to prefer plant leaves to plant stems (Arnold, 1960, 1963; Cook & Harris, 1950; Reppert, 1960) and moister and younger biomass over drier and older biomass (Arnold, 1963; Cook et al., 1956; Cowlishaw & Alder, 1960; Milton, 1953; Reppert, 1960; Stapledon, 1934). These general rules render some plants less palatable to grazers, and observed grazing behavior shows that animals will graze elsewhere if suitable plants are unavailable (Arnold, 1964).

Despite possible deleterious impacts of grazing with domestic animals, grazers can be used effectively as a restoration tool. Many factors must be considered with targeted grazing, including, but not limited to, species of grazer, stocking rate, duration of grazing, season of grazing, targeted plant species, and extent of dominance of targeted plant species (Budd & Thorpe, 2009). Non-native species populations can be reduced by grazing in short pulses and leaving long periods of rest between grazing (Budd & Thorpe, 2009). In a Nevada study of *Bromus tectorum*, a non-native grass, grazers reduced 80-90% of standing biomass, and within two years changed the ecosystem dynamics from a landscape where *B. tectorum* was the dominant plant to a landscape where *B. tectorum* was only a component (Diamond et al., 2017). Grazers can even increase the diversity of a site by providing necessary disturbance, as in the case of a California riparian zone with a historical legacy of grazing (Marty, 2005). With careful planning and set restoration goals, targeted grazing can be a useful biological tool for restoration.

Invasive Plant Dynamics

Herbicide, mulch, and microtopography can all contribute to reducing the presence of non-native species. Habitat alteration, oftentimes due to urbanization and agriculture, can displace native species and/or encourage non-native species invasion (Anderson & Inouye, 2001; Gurevitch & Padilla, 2004). Habitat alteration is well-documented across semi-arid North America, where low sagebrush (*Artemisia spp.*) shrubland biomes are often converted to farms or ranches, and non-native species invasions follow (Anderson & Inouye, 2001). Sagebrush shrublands are often in dry, windy, high-elevation basins with calcareous parent materials. Here, dwarf shrubs are common and are interspersed with rhizomatous and bunch grasses and low-growing forbs. These types of plant communities are susceptible to overgrazing and non-native grasses can often outcompete native grasses and forbs (Gonzales & Clements, 2010).

Vacant Niche Hypothesis

Invasive plant invasions can be explained, in part, by the vacant niche hypothesis. In this case, we focus on the vulnerability of low sagebrush shrubland biomes to invasion by winter annual plants (Hutchinson, 1957; Walker & Valentine, 1984). The hypothesis states that within any ecosystem, there exists uncolonized niches that may be filled by introduced species which may or may not displace native species or cause native species extinction. Here, we suggest using physical, chemical, and biological means to reduce non-native plant populations to create vacant niches where native plants can fill in. Low sagebrush shrubland ecosystems are naturally full of empty niches; sagebrush in the

American West finds its fullest extent at about 38% canopy cover (Anderson & Inouye, 2001). Patches of bare soil may not be able to support vegetation at all times of the year due to limited soil moisture and/or nutrients, but invasive plants often have different phenologies than native plants. For example, winter annual plants germinate in the fall and maintain aboveground leaves and root systems throughout winter. Winter annuals have an earlier maturation phenology than native perennials, which may allow them to capitalize on early spring soil water and nutrients that otherwise might be available to native perennial plants later in the growing season. Sagebrush-steppe biomes are the dominant vegetation type of semi-arid regions of North America (Anderson & Inouye, 2001), and their vacant niches and susceptibility to invasion by non-native species (Bradley, 2010) leave large areas of the American West at risk of degradation.

Restoration in the Gardiner Basin of Yellowstone National Park

Gardiner Basin Climate

In 2008 the National Park Service launched a pilot revegetation project on ~20 hectares dominated by non-native plants in the semi-arid Gardiner Basin, a region of northern Yellowstone National Park that lies within the Paradise Valley near Gardiner, Montana (UTM coordinates [Zone 12T]: 519187.3, 4988473.5).

A statewide Montana Climate Assessment found that precipitation patterns in southwestern Montana have not significantly changed from 1950 to 2015 (Whitlock et al., 2017). Southwest Montana is characterized by ranges of the Northern Rocky Mountains, broken up by large, semi-arid basins. Vegetation in the region varies from shortgrass prairie and sagebrush steppe to forested areas, to sub-alpine and alpine regions. A more local dataset from Gardiner showed a declining precipitation trend between 1956 and 2017 (Figure 2; adjusted $R^2 = 0.14$, $y = -1.12x + 292.16$, $p=0.02$). While regionally, the precipitations patterns are not changing, Gardiner lies in a semi-arid rain shadow of the Gallatin Mountains, and may be more sensitive to climatic shifts. This is a truncated dataset; thirty of the 61 years of data available were excluded because one or more months were missing data. There is high inter-annual variability (coefficient of variation = 20.5%) in this dataset, which could affect plants' ability to establish in the lower than average growing seasons. Overall, these data show the average annual precipitation over this period to be 259 mm.

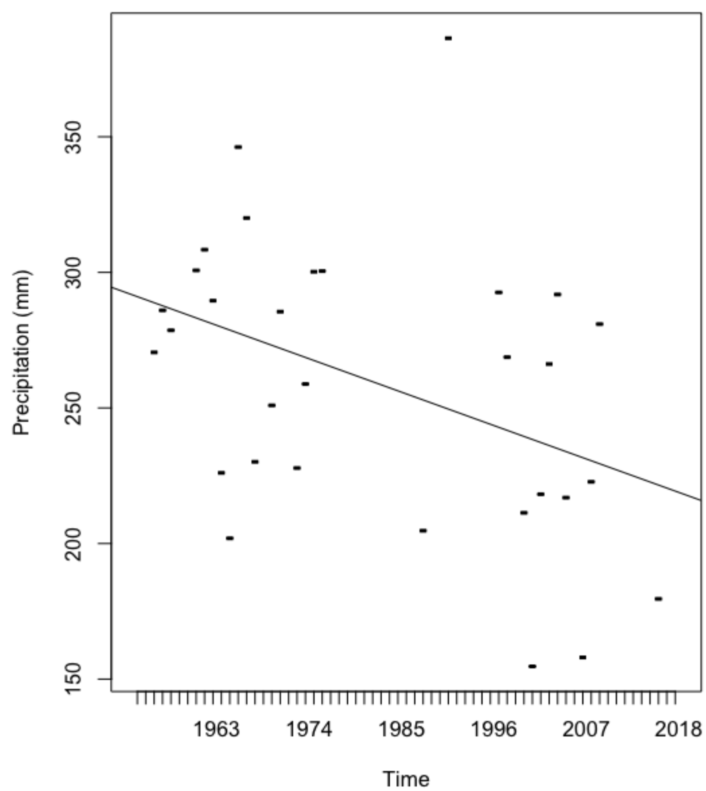


Figure 2. Mean annual precipitation (mm) in Gardiner, Montana, period 1956-2017.

The hottest month in Gardiner is July with a maximum average temperature of 30°C, while the coldest month is January with a minimum average temperature of -10°C (Table 1). The soil water deficit was calculated with the Penman-Montieth method for deducing potential evapotranspiration, which includes parameters such as elevation, latitude, and solar radiation (Tercek & Thoma, n.d.; Thoma pers. comm.). The soil water deficit reflects the difference between actual evapotranspiration and potential evapotranspiration. The greatest predicted deficit is in July (153 mm) and the smallest is in January (6 mm). The growing season deficit in May- July (78-153 mm) is more intense than the deficit in February-April (9-45 mm). An estimated annual water budget of the site shows soils in a water deficit every month of the year, (Table 1). This site is at the low end of the aridity index with a mean AI_u of 0.24 (1990-2017; Climate Analyzer, 2018) and a mean Bailey Moisture Index S of 2.94 (1990-2017 excluding 1991 and 2000; Climate Analyzer, 2018).

Table 1. Mean monthly precipitation (Precip; mm), minimum temperature (Tmin; °C), maximum temperature (Tmax; °C), period 1956-2017, soil water deficit (mm), and potential evapotranspiration (PET; mm) for the Gardiner Basin, period 1990-2017 (Climate Analyzer, 2018).

Month	Precip (mm)	Tmin (°C)	Tmax (°C)	Soil H_2O Deficit (mm)	PET (mm)
January	11.3	-9.7	0.6	5.9	14.3
February	8.5	-7.9	3.5	8.9	26.8
March	16.5	-4.4	8.3	23.9	57.7
April	17.5	-0.8	13.3	45.1	83.2
May	38.6	3.6	19	77.6	124.0
June	36.9	7.7	24.7	110	155.4
July	26.8	11.2	30.2	152.9	182.9
August	22.3	10.4	29.2	143.8	162.9
September	22.7	5.8	23.4	94.8	110.2
October	21.8	1	15.7	44.6	62.3
November	17	-5	6.1	18	28.4
December	12.8	-8.8	0.9	7.2	14.2

Gardiner Basin History

Glaciers. The Bulldale and Pinedale glaciations were the two most recent glaciation events in the Northern Rocky Mountains, with maximum glacial extent occurring about 191,000 and ~20,000 years ago, respectively (Pierce et al., 2014). During the most recent Pinedale glaciation, the Gardiner Basin was covered in ice ~2 kilometers thick based on a reconstructed glacier mass balance for the northern Yellowstone outlet glacier (Pierce et al., 2014). As this glacier was retreating south, shifts in the pollen record suggest warming and drying conditions in the northern Yellowstone area that led to a succession of vegetation communities: tundra was succeeded by spruce parkland, which was replaced by closed subalpine forests, which, in turn, were replaced by sagebrush-steppe at lower (warmer) elevations and open mixed forests at higher (cooler) elevations (Pierce et al., 2014). The initial transitions in postglacial plant communities were likely sudden, as evidenced by giant, parallel ripple marks of water-deposited boulders associated with sudden, high-energy floods from glacially dammed and landslide-dammed lakes in the Gardiner Basin (Pierce et al., 2014).

Grasslands and Ungulates. The Gardiner Basin supports eight native ungulates whose geographic ranges include Yellowstone National Park (bighorn sheep [*Ovis canadensis]*, bison [*Bison bison*], elk [*Cervis canadensis*], moose [*Alces alces*], mountain goat [*Oreamnos americanus*], mule deer [*Odocoileus hemionus*], pronghorn [*Antilocapra americana*], and white-tailed deer [*Odocoileus virginianus*]). The fossil record suggests that woodlands were converted to biomes that encompass low sagebrush shrublands and short-grass prairies, starting ~18 million years ago in the Miocene era (Janis et al., 2002). At this time, the paleoclimate in North America was undergoing changing regional temperature and precipitation patterns. In addition, the atmospheric carbon dioxide shifted from ~180 to ~350 parts per million before stabilizing at pre-industrial levels of ~285 parts per million (Janis et al., 2002; Pagani, 1999). Concurrently, semi-arid regions were expanding across North America. A changing climate coupled with rising then falling CO_2 concentrations may have triggered a conversion of C_3-dominated woodland habitats to open grasslands dominated by the C_4 photosynthetic pathway better adapted to survive in lower CO_2 environments (Janis et al., 2002; Pagani, 1999). A positive feedback loop is thought to have been created between the density and species richness of grazers and the quality of grassland forage; fast-growing grasses with higher carbon to nitrogen ratios tend to be preferred forage over slow-growing woody C_3 plants like sagebrush species (Janis et al., 2002). In the semi-arid West, low sagebrush shrublands host both C_3 and C_4 plants that compete directly for water and nutrients, albeit via different photosynthetic mechanisms. A restored Gardiner Basin might be dominated by C_4 plants, but its current condition is more C_3, with a mix of C_3 and C_4 plants. This could help explain the current low forage value for grazing ungulates.

Humans. The Montana-Yellowstone Archaeological Project found evidence of seasonal occupation by Pelican Lake Native Americans at least 11,000 years ago, suggesting humans first settled in the Gardiner Basin as the ice retreated (MacDonald et al., 2010). While humans have inhabited this site for millennia, the most intensive land use changes in the Gardiner Basin likely only began ~150 years ago with the arrival of the railroad to Cinnabar, MT, on September 1, 1883 (MacDonald, 2008; Appendix A, Figure A2; DOI: 10.5281/zenodo.1213337). The railroad was expanded to bring tourists to Yellowstone National Park, which was established a decade earlier on March 1, 1872. The low sagebrush shrubland surrounding Cinnabar was converted to human settlements and agricultural land (Appendix A, Figures A3-A7; DOI: 10.5281/zenodo.1213337). In 1903, just two decades after the town's founding, the train depot was relocated ~5 kilometers south (upriver) to present-day Gardiner, and Cinnabar was dismantled and abandoned.

Grazing Pressure. Ungulate grazing pressure in Yellowstone National Park was artificially elevated following the local extirpation of large carnivores (*e.g.*, the gray wolf [*Canus lupis*]) in 1926 and National Park Service "taming" practices such as established feedlots for the American black bear (*Ursus americanus*) and the grizzly bear (*Ursus arctos horribilis;* Bangs & U.S. Department of the Interior Fish and Wildlife Service, 1994; Phillips et al., 1998; Pritchard, 1999; Reichard, 2016) initiated around 1900. Consequently, the elk population grew to a density that was oftentimes greater than the carrying capacity of the Yellowstone northern winter range, which varies based on the year between ~10,000 and 18,000 individuals (Coughenour and Singer, 1996). Widespread "grazing lawns" in contrast to aspen- or shrub-dominated exclosures are still evident today (Frank and Groffman, 1998). Elk populations in Yellowstone National Park were the highest in the late 1980's at over 20,000 individuals (Coughenour and Singer, 1996) but have since decreased to a population ~5,350 individuals as of the 2016-2017 winter season, likely due to closure of the bear feedlots in 1970, the reintroduction of gray wolves in 1995, and generally better management practices (Houston, 1982; Meagher, 1973; Montana Fish, Wildlife & Parks, 2017; Pritchard, 1999; Smith et al., 2003). The legacy of overgrazing in the northern Yellowstone area could persist for decades (Abril & Bucher, 2001).

Gardiner Basin grazers may be contributing to its present and ongoing degradation. In the semi-arid West, ungulates selectively graze seed heads of native grasses but avoid non-native species, many of which lack natural predators and are relatively unpalatable after the seed head develops (Morrison & Hay, 2011). Such selective grazing may thereby have reduced the competitive advantages of native species, which could have, in turn, encouraged the current dominance by non-native species (Moretto & Distel, 1999; Schwartz & Ellis, 1981). Overgrazing may have led to the decline in shrub cover, although other factors such as climate change and land conversion likely contributed in transforming the low sagebrush shrubland (likely dominated by sagebrush and rabbitbrush) to grasses, both native and non-native (Appendix A, Figures A3-A7; DOI: 10.5281/zenodo.1213337).

Restoration Efforts. In 1932 land managers at Yellowstone National Park identified the Gardiner Basin as critical winter habitat for native ungulates, and the National Park Service bought private lands and used eminent domain privileges to acquire the Gardiner Basin for a large-scale revegetation project to improve the quality of forage degraded by human use. Initially, the National Park Service planted the non-native perennial grass crested wheatgrass (*Agropyron cristatum*), believing it would provide better forage. By the 1950s, the Gardiner Basin was dominated by crested wheatgrass. More recently vegetation within the Gardiner Basin further degraded to annual non-native species such as desert alyssum (*Alyssum desertorum*) and annual wheatgrass (*Eremopyrum triticeum*; Renkin, 2014) that is observed today. As a result, the degraded grasslands support fewer grazers, which may have other deleterious impacts like increasing human-wildlife interactions as grazers must travel further north for food up the increasingly developed Paradise Valley.

According to National Park Service policies (Section 4.4.2.2: Restoration of Native Plant and Animal Species), the National Park Service must attempt to restore species disappeared or diminished by anthropogenic causes (U.S. Department of the Interior National Park Service, 2006). In addition, the National Park Service has a legal obligation to control any species designated as a “noxious weed,” which is a designation given at the state and federal level for species that cause economic, agronomic, and ecological losses. Although the dominant plants in the Gardiner Basin are not designated “noxious weeds”, they are non-native and aggressive, which could place them on the noxious weed list in the future if their dominance becomes too widespread or causes too much economic, agronomic, or ecological loss. This inspired a voluntary 2008 revegetation proposal to restore the historical plant community and provide improved forage for ungulates. The complex history of disturbance in the Gardiner Basin requires intensive and thoughtful revegetation techniques to restore ecosystem services, such as higher quality forage for native ungulates.

The Yellowstone National Park restoration project identified four sites with high potential for restoration (Renkin, 2014). These sites, one of which was the old Cinnabar townsite, were later converted to agricultural fields before being dominated by non-native species. The sites were enclosed with 2.4-meter-high wildlife fencing in 2006 to prevent ungulate herbivory while native plants were establishing. Two of the four sites were located on river terraces of the Yellowstone River comprised of younger soils characterized as silty clay loams, while two sites were at a slightly higher elevation and characterized by older, loam soils (Renkin, 2014). Management differed across sites, partly because the plant communities on the upper river terrace were dominated by non-native winter annuals, while the lower river terrace sites were dominated by both summer and winter annual plants that may be capitalizing on their proximity to the Yellowstone River and potentially greater water stores and available soil water moisture (Hellquist et al., 2011; Renkin, 2014). The National Park Service, unfortunately, has had relatively little success in establishing native vegetation since the start of the pilot project in 2008.

The National Park Service has tried a variety of methods to prepare the sites for revegetation. After fencing, all sites were treated with a variety of post-emergent herbicides (*e.g.*, Roundup®, Express®, Plateau®). All sites were also planted twice with cover crops—winter wheat (*Triticum aestivum*) was seeded in fall and barley (*Hordeum vulgare*) seeded in spring—to increase soil organic matter and reduce non-native species populations. Cover cropping was implemented for three years with concurrent non-native species management. In the Cinnabar exclosure in October 2012 and March 2013, prescribed burns on cover-crop stubble reduced the seed bank of *A. desertorum* in 2011 by 99% and in 2012 by 47% (Renkin, 2014). However, because prescribed fire did not carry well, further burns were discouraged. A comprehensive and chronological record of seeding rates at individual locations is not known to exist. Records starting in 2013, though, indicate drill seedings containing 50% bluebunch wheatgrass (*Pseudoroegneria spicata)*, 30% Sandberg bluegrass (*Poa secunda)*, 15% slender wheatgrass (*Elymus trachycaulus)*, and 5% green needlegrass (*Nassella viridul)* at 12-inch rows at a depth of ¼- to ½-inch below the surface at a rate of about 20 kg/ha. Drill seeding, as well as intermittent broadcast seeding of sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* spp.), greasewood (*Adenostoma fasciculatum*), and basin wildrye (*Leymus cinereus*), as well as other undocumented forbs (Renkin, 2014; Klaptosky, pers. comm.) has continued throughout 2017 with concurrent non-native species management. Non-native plants drastically outnumber native plants, and native plant species establishment is low.

Non-Native Species Dominance. Non-native plant proliferation may be difficult to control due to one or a combination of three general principles of invasion: (i) invasive traits, (ii) propagule pressure, and (iii) invasibility of the novel environment (Barney et al., 2008; Davis & Pelsor, 2001; Lockwood et al., 2005; Rejmanek, 2005). These three factors are not the only drivers of non-native plant invasions but can help clarify competitive advantages of non-native plants over native plants.

Desert alyssum, the dominant plant species in the Gardiner Basin, is a winter annual plant that is increasingly widespread in arid to semi-arid regions in the American West (Mosley, 2014). Its native ranges include Africa, Asia, and Europe (Jacobs, 2012), but little is published about this plant in non-native settings. What is known, however, is that desert alyssum requires disturbance for population expansion (Jacobs, 2012), which helps explain its monoculture-like dominance in the Gardiner Basin (Appendix A, Figure A8; DOI: 10.5281/zenodo.1213337).

Invasive Traits. Desert alyssum can emerge as both a winter and a spring annual. By germinating after fall moisture and maintaining basal leaves and roots through winter, desert alyssum can complete its life cycle and set seeds sooner than perennial plants. This trait may give desert alyssum access to early spring soil moisture that perennial plants may not be ready to use due to their slower phenology.

Propagule Pressure. Desert alyssum's propagule pressure adds to the difficulty of native plant revegetation. The Gardiner Basin hosts desert alyssum seed densities averaging 4.5 seeds cm^{-2} (range: 1.4 to 9.0) inside exclosures and 2.6 seeds cm^{-2} (range: 1.8 to 4.5) outside exclosures. Just 3 seeds cm^{-2} would translate to roughly 50 million seeds per hectare (Table 2; Hamilton, 2014).

Table 2. Seed bank density of *Alyssum desertorum* (seeds cm^{-2}) and corresponding standard errors (SE) inside and outside the Cinnabar exclosures (unpublished data printed with permission from Bill Hamilton, Washington and Lee University).

Date	Inside Exclosure	SE	Outside Exclosure	SE
5/1/07	*NA*	*NA*	2.0	0.2
10/1/07	*NA*	*NA*	2.4	0.3
5/1/09	1.9	4.0	1.8	0.4
10/1/09	1.4	5.0	2.6	0.2
5/1/10	7.0	2.0	1.8	0.3
10/1/10	5.0	4.0	2.0	0.4
5/1/11	2.0	3.0	2.2	0.4
10/1/11	1.6	4.0	2.8	0.3
5/1/12	1.4	3.0	2.0	0.2
10/9/12	9.0	1.5	3.2	0.3
5/1/13	8.5	1.8	2.8	0.3
10/1/13	3.0	1.0	3.1	0.4
5/1/14	5.2	1.1	4.5	0.4
5/1/15	8.5	2.5	3.8	0.4
Mean	4.5		2.6	

While prescribed burns on the study site reduced seed bank densities of desert alyssum from 800 plants/m^2 to 300 plants/m^2, because these burns did not carry well and posed threats to surrounding areas, they have not been attempted since (Hamilton, 2014; Renkin, 2014). A pre-emergent herbicide with high residual activity has been considered for its ability to reduce non-native species propagule pressure by killing germinating seeds in the soil, thus reducing the seed bank. Such herbicides are applied on top of drill-seeded grasses to reduce non-native species populations, or on top of established perennials to stop new germination. The National Park Service has been investigating the effects of Esplanade® 200 SC (Bayer CropScience LP, Monheim am Rhein, Germany), whose active ingredient is Indaziflam at 19.05%. It may reside in the soil for 3 to 4 years after application, which may help grasses establish without competition from non-native plants. Early Esplanade® 200 SC trials in the Gardiner Basin have resulted in 98% efficacy at controlling annual wheatgrass and 100% efficacy at controlling desert alyssum at application rates of ~220 milliliters hectare^{-1} (3 ounces acre^{-1}) and ~365 mL hectare^{-1} (5 ounces acre^{-1}) rates without any injury to native perennial grasses (Rice, 2018).

<u>Invasibility of the Novel Environment.</u> Finally, degraded soil conditions, including areas of high salinity and low soil organic matter, have been documented at the Gardiner Basin restoration site (Appendix B, B1 & B2; DOI: 10.5281/zenodo.1213337). In some soil samples taken from the Reese Creek sites, sodium adsorption ratios reached as high as 39.2 (Appendix B, B2; DOI: 10.5281/zenodo.1213337), well over the optimal plant growing range of 13 based on a circumneutral pH (Brady & Weil, 2010). Soil organic matter at both Cinnabar and Reese Creek sites ranged from 1.1% to 3.8% with an

average of 2.1% (this study; Appendix B, B1 & B2; DOI: 10.5281/zenodo.1213337). In order to establish desirable plants, land managers must improve the underlying environmental conditions with a process-based ecological framework that focuses on succession; otherwise, treating symptoms instead of underlying ecological causes risks compromising long-term restoration success (Krueger-Mangold et al., 2006; Sheley & Krueger-Mangold, 2003).

An awareness of historical influences as well as careful site preparation, including consideration of physical, chemical and biological techniques such as those detailed above are keys to a successful restoration project. Even the most well-meaning restoration projects, like the National Park Service revegetation project that was informed by recommendations from professionals in agencies, industry, and academia (Renkin, 2014), can be stalled by a number of obstacles. The next chapter describes a field study where the best site-specific combination of restoration treatments based on their abilities to reduce non-native species and encourage native plant establishment were evaluated in the context of the projected likelihood of increased aridity (Whitlock et al., 2017).

CHAPTER TWO

FIELD STUDY

Re-Establishing Native Species in Northern Yellowstone National Park

Introduction

Restoration success in semi-arid environments can be complicated by the frequency and intensity of natural disturbances such as grazing, wildfire, and drought, all of which can be intensified by human activities. Plant establishment and the longevity of restoration success in semi-arid regions can therefore depend on restoration techniques that protect vegetation from herbivory and promote its initial ability to capitalize on scarce growing-season precipitation. Of course, adequate growing season water is required for post-disturbance growth in semi-arid regions, and as climate changes, precipitation may be insufficient to sustain or restore native plant communities. Emphasizing soil water storage in a restoration context could be especially beneficial in semi-arid and arid regions, which account for nearly one-third of global land area (Salem, 1989). Thus, restoration techniques that help build longer-term soil water storage capacity may help establishing plants meet their needs and contribute to broader-scale success in semi-arid restoration projects. Three of these techniques include mulch, microtopography, and herbicide.

Surface mulching is a tool used to maintain soil water by reducing evaporative losses, particularly when rainfall is low (Groenevelt et al., 1989; Ji & Unger, 2001). On a short time scale, mulch residues decrease evaporation and lengthen the amount of time necessary for soil to dry (Bond & Willis, 1969). Moisture savings from mulching could be one explanation why mulch has increased crop yields in agronomic settings (Jones Jr. et al., 1969).

Microtopography is a lesser-studied technique with the potential to increase growing season water availability by spatially concentrating water. Microtopography is soil surface roughness on the decimeter to meter (m) scale made up of micro-highs and micro-lows (Kishné et al., 2014; Thompson et al., 2010; Figure 1). Microtopography can help re-establish vegetation in four ways. First, micro-lows can collect a greater volume of precipitation, either as rain, overland flow (Kishné et al., 2014), or snow (Sturm & Holmgren, 1994). Compared to surrounding areas, the basin-like shapes of micro-lows may increase soil water infiltration (Dunne et al., 1991; Thompson et al., 2010). Infiltration may also increase if micro-lows store snow that eventually contributes to snowmelt rather than sublimation. Second, micro-lows can retain a deeper and colder snowpack, which may slow the timing of snowmelt, choking out winter annual species by ice cover or saturated soils. Killing winter annual species may thus reduce competition with desirable summer annual or perennial species (Appendix A, Figure A1; DOI: 10.5281/zenodo.1213337). Micro-lows thereby mitigate growing season aridity by giving plants access to soil water when water in the unmanipulated areas has already been transpired or evaporated to the atmosphere. Third, micro-lows can serve as catchment basins for aeolian dust, organic matter, and seeds (Fick et al., 2016). Microtopography can also increase species diversity, benefiting non-generalist seeds by niche differentiation (Moser et al., 2007). Seeds in micro-lows may form small “nucleation islands" (Corbin & Holl, 2012) by capitalizing on the water and nutrients held there. As these plant islands mature, they may then provide a seed source to surrounding barren areas until individual nucleation islands connect (Corbin & Holl, 2012). Lastly, micro-lows can serve as nurse sites, providing microclimate protection to seeds from the higher wind speeds and greater insolation of unmanipulated areas (Flores & Jurado, 2003).

Management, and ideally eradication, of non-native species on restoration sites is a priority to ensure adequate soil resources, including root zone moisture, are available for native plants. Herbicides are a tool for quickly and efficiently killing non-native plants and curbing competition for limited soil water resources. By reducing the soil water lost via transpiration from non-native species, there is greater soil water available for desired seeded species. Herbicides should be specific to the restoration project and the non-native species. For example, some herbicides target only broadleaf plants without harming grasses. Herbicides with residual effects can also be helpful in restoration settings to reduce the effort involved in continual spraying and to ensure that any non-native, herbicide-targeted seeds in the seed bank that germinate after spraying will die. Overall, the goal with herbicides is simple: kill unwanted, non-native species to allow more soil water for desirable, seeded species.

The invasion of non-native plants across the semi-arid western United States has been well documented (Knapp, 1996; Lesica & DeLuca, 1996; Shafroth et al., 2005). In the United States, which has a total land area of about 1 billion hectares, an estimated 51 million hectares have been invaded by at least one ecosystem-altering non-native plant (DiTomaso, 2000; Duncan et al., 2004), with species in some contexts spreading at a rate of 14% per year (Westbrooks, 2017). In some cases, disturbances such as overgrazing have inadvertently converted existing plant communities dominated by perennial grasses into novel communities dominated by annual grasses (Moretto & Distel, 1999). In other words, disturbance or degradation might be facilitating the spread of non-native species (MacDougall & Turkington, 2005). In semi-arid regions, winter annual plants may be filling a natural vacant niche in the ecosystem (Hutchinson, 1957; Walker & Valentine, 1984). By germinating while perennial plants are in dormancy, annual plants can capitalize on little to no competition, sufficient water, and newly mineralized nutrients (Brooks et al., 1998). Perennial plants may then suffer from low emergence or reduced growth as annual plants pre-emptively reduce soil water and nutrients. In the case of winter annual, non-native species (*e.g.*, *Alyssum desertorum* [Desert alyssum], *Eremopyrum triticeum* [annual wheatgrass]), such plants could grow viable seed prior to the emergence of perennial, native plants, and in cases, deplete soil water and nutrients to suboptimal levels for native perennials. Therefore, eradicating non-native winter annuals could lead to greater soil moisture availability for native perennials.

Yellowstone National Park's Gardiner Basin represents a microcosm of these challenges. Native Americans first occupied the Gardiner Basin at least 11,000 years ago, although intensive land use likely began with the arrival of the railroad to the town of Cinnabar, Montana, in 1883 (MacDonald, 2008; Appendix A, Figure A2; DOI: 10.5281/zenodo.1213337) about 5.5 km northwest of the town of Gardiner. Ensuing human settlement and conventional agriculture converted the low sagebrush shrubland biome to monocultures of annual non-native species (Renkin, 2014; Appendix A, Figures

A3-7; DOI: 10.5281/zenodo.1213337). Cinnabar was abandoned in 1903; in 1932 the National Park Service used eminent domain privileges with the intention to restore the Gardiner Basin for winter forage and as a migration thoroughfare for the largest natural concentration of land mammals in the lower 48 states (National Park Service, 2018; Renkin, 2014). To this day, the Gardiner Basin remains a critical area in which inadequate forage for ungulates, for whom the area was originally protected, was documented as early as 1938 (Grimm, 1939). In 2008 the National Park Service launched a pilot restoration project intended to “restore a mosaic of native plant communities that provides wildlife habitat and forage” and to “restore functioning water, soil, and energy cycles; soil properties; and a sustainable native shrub-grassland plant association similar to the site potential,” all in concordance with National Park Service guidelines requiring non-native plant control and restoration of human-caused degradation (Renkin, 2014; U.S. Department of the Interior National Park Service, 2006). Unfortunately, the site has had unexpectedly low native plant establishment, although no plant monitoring program was implemented so exact densities in response to treatments are not known. However, years of efforts of herbicide application and seeding with little success has kept soils relatively bare (Renkin, 2014). Soil monitoring has shown that areas dominated by non-native plants have lower soil organic matter, soil moisture holding capacity, net ecosystem productivity, soil respiration rates, and soil community diversity (Renkin, 2014).

Because of the potential for herbicides to work synergistically with other dryland restoration approaches such as mulch and microtopography, our overall objective with this study was to explore how three specific treatments (herbicide, mulch, and microtopography) and combinations thereof might impact native and non-native plant species in the Gardiner Basin. We sought to quantify the effects of treatments on plant canopy covers and densities. Specifically, we aimed to decrease canopy cover and density of undesirable, non-native species while increasing the canopy cover and density of native species.

The hypotheses for this study were as follows:

(i) Herbicide, mulch, and microtopography treatments will increase the canopy cover and density of native plants.

(ii) The three-way combination of herbicide, mulch, and microtopography will be the most effective treatment at both increasing the canopy cover and density of native plants while having the opposite effect on non-native plants.

(iii) Micro-low plots, as compared to unmanipulated control plot or adjacent micro-high plots, will have greater volumetric soil water content.

(iv) Micro-low plots, as compared to unmanipulated control plots or adjacent micro-high plots, will support greater canopy covers and densities of native plants

Methods

Study Sites. Three study sites, Cinnabar (CIN [UTM coordinates Zone 12T: 519187.3, 4988473.5]), Reese Creek North (RCN [518279.5, 4989746.2]), Reese Creek South (RCS [518345.5, 4989691.8]) were chosen within the Yellowstone National Park

Gardiner Basin restoration project, about 7 km northwest of the Gardiner entrance to the park and on the western river terraces of the Yellowstone River at an elevation of ~1580 m (Figure 3). Between 2008 and 2009, ~9 hectares at CIN, ~3.5 hectares at RCN, and ~4.5 hectares at RCS were enclosed with 2.4-m tall fence that excludes wildlife to allow seedlings to establish without ungulate grazing pressure. Although historical vegetation surveys do not exist, the site was likely originally dominated by *Artemisia nova* (black sage), *Artemisia arbuscula* ssp. *longiloba* (little sagebrush), and *Chrysothamnus* spp. (rabbitbrush spp.) with an understory of graminoids and forbs. More recent plant surveys (this study) and a National Park Service botany team have also found *Opuntia polyacantha* (prickly pear cactus) and *Sphaeralcea ambigua* (scarlet globemallow). Today, the non-native forb *Alyssum desertorum* (desert alyssum) as well as three non-native grasses, *Agropyron cristatum* (crested wheatgrass), *Bromus tectorum* (cheatgrass), and *Eremopyrum triticeum* (annual wheatgrass) dominate the vegetative community. The soils mapped at the study site were Mollisols of the Greyback series in a glacial trough valley bottom (Rodman et al., 1996); soils on the lower river terrace were sandy loams, while upper river terrace soils were loams or sandy clay loams (Appendix B, B1 & B2; DOI: 10.5281/zenodo.1213337).

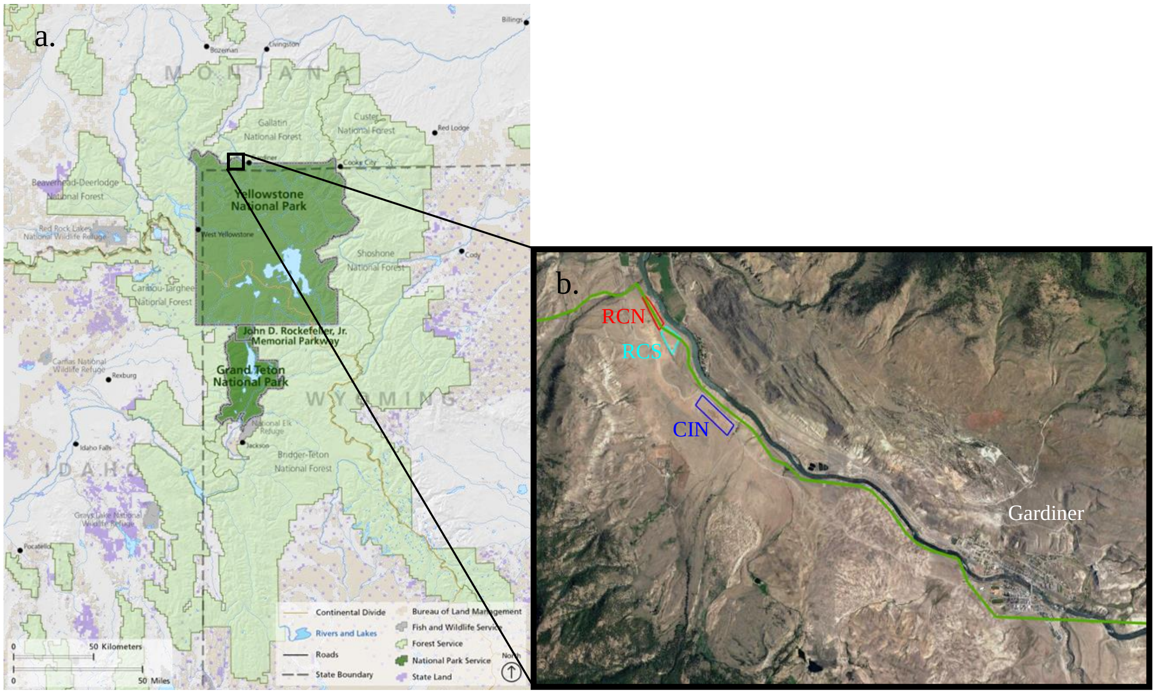


Figure 3. a. The Greater Yellowstone Ecosystem (Yellowstone National Park, 2018) showing the study location near Gardiner, Montana. b. Study sites along the Yellowstone River in the Gardiner Basin.

Long-term annual air temperatures and precipitation in the Gardiner Basin have averaged 7.5° C and 259 mm (1956-2017; 35 years of temperature data and 30 years of precipitation data were excluded due to one or more months of missing data; Climate Analyzer, 2018). Temperatures show an increasing trend, and precipitation shows a decreasing trend, but with high inter-annual variability (temperature model fit: $p<0.001$; coefficient of variation = 12%; precipitation model fit: $p<0.001$; coefficient of variation = 21%). Furthermore, precipitation is not distributed evenly across the year. On average, the months receiving the greatest precipitation are May (39 mm; ~15% of annual precipitation) and June (37 mm; also ~15% of annual precipitation), and the months receiving the least are January (11 mm; ~4% of annual precipitation) and February (9 mm; ~3% of annual precipitation). We modeled monthly water budgets for this site as the difference between actual evapotranspiration (AET) and potential evapotranspiration (PET: estimated via the Penman-Monteith method; Thoma et al., 2015; Tercek & Thoma, n.d.; Thoma pers. comm.).

Our water budget (Figure 4c) shows these Gardiner Basin soils are in a water deficit (AET<PET) every month of the year (period from 1990 to 2017), with the greatest deficit in July (153 mm) and the smallest in January (6 mm). The growing season deficit for native summer perennials (May- July: between 78-153 mm) is more intense than the deficit for winter annuals (February-April: between 9-45 mm; Figure 4c). On an annual basis, these average monthly deficits sum to 733 mm (Figure 4c). Thoma et al. (2015) have also estimated trends in water deficits for 11 weather stations near the northern portion of Yellowstone National Park over time (1980-2011); after splitting the stations into three elevational categories (<1980 m, 1980-2440 m, >2440 m), only the lowest elevation weather stations, including Gardiner, showed a statistically significant increase in modeled water deficits over time, from ~75 mm in 1980 to ~140 mm in 2011.

While it would be nearly impossible for there to be any vegetative growth under conditions of the perennial soil water deficits we have modeled, plants have evolved numerous adaptations that enable them to take up and transpire water even under drought conditions (Bohnert et al., 1995). Furthermore, micrometeorological approaches to estimating potential evapotranspiration do not always yield close matches to actual evapotranspiration, which can vary widely over very short distances (meters) and timeframes (seconds). Unlike precipitation, this variability in evapotranspiration is difficult to measure even with sophisticated eddy covariance approaches (Ha et al., 2014). Thus, we provide this estimate of soil water deficits to underscore the severe challenges of dryland restoration approaches in this Gardiner Basin context.

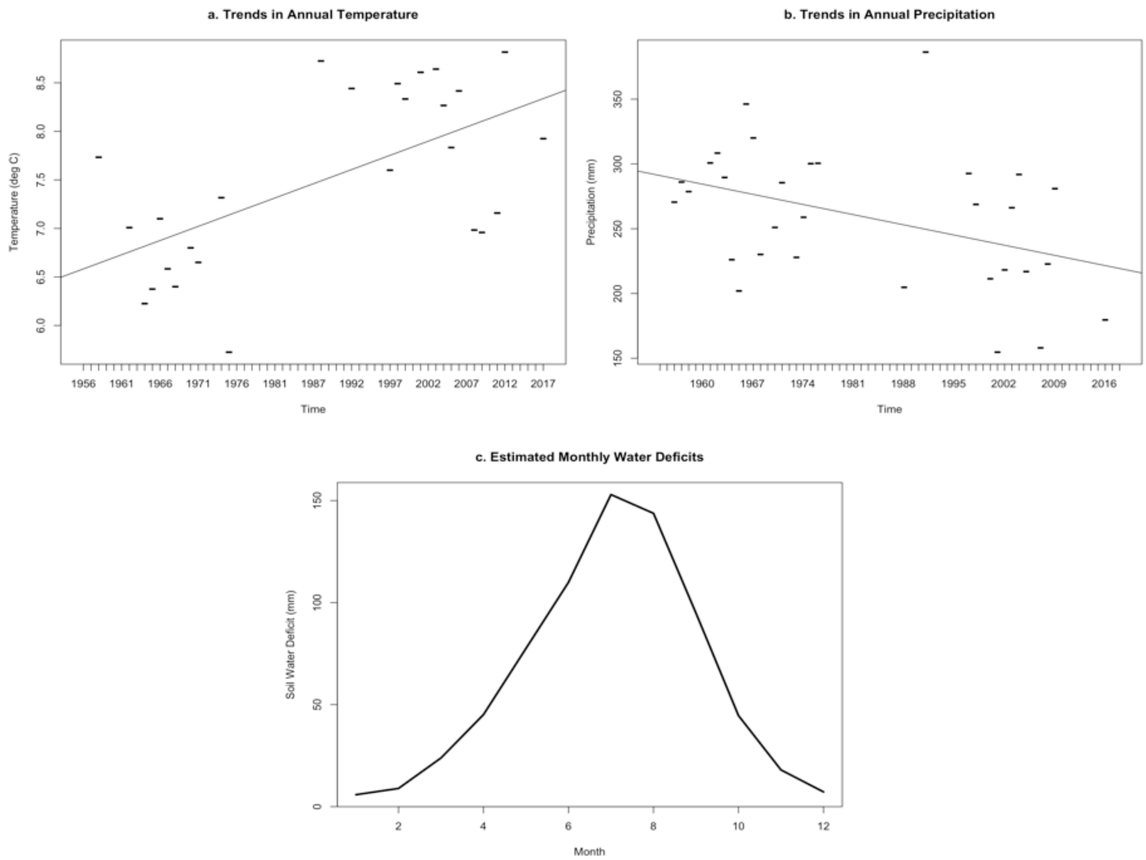


Figure 4. a. Trends in annual temperature, 1956-2017 with years with missing data excluded; b. Trends in annual precipitation, 1956-2017 with years with missing data excluded; c. Estimated monthly water deficits 1990-2017, (Climate Analyzer, 2018).

<u>Experimental Design.</u> We established five blocks within each site in areas where no individuals of native species were found. Each block, 4 m x 2 m, consisted of eight 1 m by 1 m plots, each one randomly assigned to one of eight treatments (codes are shown in [brackets]):

(1) herbicide [H]
(2) mulch [M]
(3) microtopography [T]
(4) herbicide and microtopography [H+T]
(5) herbicide and mulch [H+M]
(6) mulch and microtopography [M+T]
(7) herbicide and mulch and microtopography [H+M+T]
(8) non-treated control [C]

In chronological order, microtopography containing six micro-highs and six micro-lows per m^2 was hand dug with a spade in summer 2016 within each microtopography plot (T, H+T, M+T, or H+M+T). Micro-lows were depressed about 20-30 cm lower than the original soil surface, where micro-highs were raised by the same amount of soil. Next, shredded red cedar mulch was applied to mulch plots (M, H+M, M+T, or H+M+T) at 100% ground cover, approximately 3 cm thick, in summer 2016. Glyphosate herbicide (diluted to 1.5%; Roundup®, Monsanto Technology LLC, St. Louis, MO) was backpack sprayed (H, H+M, H+T, or H+M+T) on November 2, 2016 to target winter annual species at a rate of 3400 g per hectare, or about 0.34 g per 1 m^2 plot. At this time, *A. desertorum* and other weeds were already growing through the mulch layer, and foliage came in contact with the herbicide. Herbicide spraying was timed to coincide with the *A. desertorum* flush that typically occurs in late fall after precipitation events but before freezing temperatures arrive. The temperature at the time of spraying was 6.1°C. Finally, all 120 1-m^2 plots (including controls) were broadcast seeded with a chest-mount seeder in March 2017 with a mix of six native species and vermiculite (Therm-O-Rock West, Inc, Chandler, AZ) as a seed carrier. The seed mix consisted of *Hesperostipa comata* (needle-and-thread grass; seeded at a rate of 7 kg pure live seed [PLS] $hectare^{-1}$), *Elymus trachycaulus* (slender wheatgrass; 7 kg PLS $hectare^{-1}$), *Poa* *secunda* (Sandberg bluegrass; 1.3 kg PLS hectare^{-1}), *Pseudoroegneria spicata* (bluebunch wheatgrass; 9 kg PLS hectare^{-1}), *Achillea millefolium* (western yarrow; 1 kg PLS hectare^{-1}), and *Artemisia frigida* (fringed sagebrush; 0.4 kg PLS hectare^{-1}). The grass seeds in the mix (*H. comata*, *E. trachycaulus*, *P. secunda*, and *P. spicata*) were grown by Bridger Plant Materials Center in Bridger, MT, between 2014 and 2017. *Achillea millefolium* and *A. frigida* were wild-collected and increased by Stevenson Intermountain Seed. We broadcast an estimated 520,000 seeds over the area of 120 1-m^2 plots, or 4,333 seeds m^{-2} (estimations based on Majerus et al., 2013, who report seeds acre^{-1}), which is about four times the recommended seeding rate to account for the site's status as a critical area and as an adjustment for broadcast as opposed to drill seeding (Majerus et al., 2013).

<u>Field Sampling Methods.</u> Canopy cover (%) was estimated by species for each of the 120 plots between July 30 and August 2, 2017, near first-year peak canopy cover for perennial natives. At the time of censusing, annual non-natives were senescent but still present. Plants were identified to species and categorized as native or non-native. For all plots with microtopography treatments, half of each 1-m^2 plot was micro-lows and half micro-highs, so canopy cover was visually estimated for micro-lows and micro-highs separately.

Inventories of plant density (number of individuals per unit area, hereafter m^{-2}) relied on visual estimates of individuals per m^2 plot binned into one of six ranges: up to 20 individuals, 20-49, 50-99, 100-299, 300-500, or >500. We report individual counts only for the lowest density category; otherwise, we report either the range midpoints as an approximation or the minimum density for the highest density category: 35, 75, 200, 400, and 500, respectively. These counts represent individual plants, not individual tillers. A representative datasheet is shown in Appendix B, B3 (DOI: 10.5281/zenodo.1213337).

We recorded volumetric soil moisture using Hobo H21 data loggers (H21-002, Onset Computer Corporation, Bourne, MA; 10HS Soil Moisture Model SSMD-M005, EC5 Soil Moisture Model S-SMC-M005) that rely on a soil's dielectric constant to report moisture as m^3 water per m^3 soil. All measurements were recorded at 1-minute intervals to capture even small precipitation events. We installed one data logger with three soil moisture probes approximately 5 cm deep at each of the three sites. At CIN we monitored soil moisture at three plots reflecting T (micro-low as well as micro-high) and C treatments with EC5 sensors; at RCN, by contrast, we monitored soil moisture at three plots reflecting M+T (micro-low [10HS sensor] and micro-high [EC5 sensor]) and M-only treatments as a "control" (10HS sensor); and at RCS, we monitored soil moisture with EC5 sensors at three plots reflecting M+T (micro-low and micro-high) and C treatments. To visualize relative shifts in soil moisture, we calculated delta values (differences) in soil moisture. At CIN, we subtracted the C data from the T micro-low and T micro-high data. At RCN, we subtracted the M data from the micro-high and micro-low M+T plots. For RCS plots, we subtracted C data from micro-high and micro-low M+T data. We also determined post-precipitation soil drawdown dynamics in soil moisture by removing data points that indicated a soil water increase. If the mean volumetric water content was greater than that of the day before, it was excluded from the drawdown analysis. All raw data are located in Appendix B (DOI: 10.5281/zenodo.1213337).

Statistical Analyses. All analyses were coded in R statistical software in the Base Package. The effects of treatments and sites on canopy cover and plant density of both native and non-native species were analyzed using two-way analysis of variance (ANOVA) and differences were determined using Tukey's Honestly Significant Difference Post-hoc (ω) test. The ω test value was calculated using the following equation:

$$\omega = q_{\alpha}, k, df \sqrt{\frac{MSE}{n}}$$

The *q* value is determined from a Studentized Range *q* Table where α= 0.05, *k* represents the number of treatment levels, and *df* is the degrees of freedom. *MSE* is the mean square error, or the residual, from the ANOVA, and *n* is the number of replications. Then, statistically significant differences between treatments and between sites were identified when the output difference of the ω test were less than the calculated ω value.

Models for both the ANOVAs and the ω tests included main effects (site and treatment) and an interaction term (site x treatment). Normality of the data was assessed with Q-Q plots and homogeneity of variance with residual plots. Statistical significance for all tests was determined as $\alpha \leq 0.05$.

Though species densities were censused as a range (*e.g.*., 50-99 individuals), the midpoint (or minimum value) of the corresponding range was used for all statistical analyses. Paired t-tests were used to compare measurements of canopy cover and density between native and non-native plants and between micro-highs and micro-lows. Soil moisture data is summarized as a response variable based on treatments stated above. These soil moisture data were not statistically analyzed due to limited replication.

Results

Our results reflect numerous intersecting categories (nine treatments [including microtopographic highs vs. microtopographic lows], three sites, native vs. non-native species) across three response variables (cover, density, soil moisture). When we refer to native species, we include all native species found at the study sites, and not just those that we seeded. Below, we outline and contextualize our cover and density results according to our statistical model: first by (i) treatment patterns; second by (ii) site patterns; and finally, by (iii) treatment by site interaction patterns. Following this review of cover and density trends, we explore topographic effects on cover as well as on soil moisture. Both treatment and site impacted canopy covers, while the interaction term did not. Conversely, the main effects and the interaction impacted plant densities.

Treatment Patterns. Total plant canopy covers (not separated between native and non-native species) were highly variable across treatments. Control plots averaged (±1 SD) 60±33% whereas treatment plots ranged from 27 to 74% (Table 3). Treatments (H: herbicide, M: mulch, T: microtopography) had a highly significant effect on canopy covers (two-way ANOVA, $p<0.001$, Table 5). Looking at the means, H treatments decreased canopy covers compared to the control (Table 3).

Mean canopy covers across all treatments was lower for native species than for non-native species (paired t-test: $p<0.001$; Table 5). Across all 105 treatment plots (excluding controls), non-native canopy cover averaged 48±23%, about 35 times that of native species. Native species canopy covers were highest in the H and the H+M treatments. Native species canopy covers were lowest in treatments receiving microtopography (T, H+T, M+T, H+M+T; Table 5).

Table 3. Mean canopy cover and density by sites (columns: Cinnabar [CIN], Reese Creek North [RCN] and Reese Creek South [RCS]) and then by treatment (rows).

Treatment (*N*=5 site^{-1})	Canopy Cover (%) Mean±SD				Density (m^{-2}) Mean±SD			
	CIN	RCN	RCS	All sites	CIN	RCN	RCS	All sites
Control	40 ± 40^{Cb}	69 ± 27^{Ba}	69 ± 29^{Ba}	60 ± 33^{A}	174 ± 197^{Cc}	479 ± 56^{Aa}	239 ± 55^{Cb}	297 ± 177^{A}
Herbicide (H)	7 ± 6^{Dc}	44 ± 9^{CDb}	53 ± 25^{Ca}	35 ± 25^{B}	16 ± 9^{Ec}	145 ± 186^{Da}	99 ± 57^{Ab}	87 ± 118^{B}
Mulch (M)	71 ± 24^{Aa}	78 ± 17^{Aa}	73 ± 24^{Ba}	74 ± 2^{A}	264 ± 193^{Ac}	460 ± 124^{Ca}	341 ± 97^{Bb}	355 ± 157^{A}
Microtopography (T)	62 ± 27^{Bc}	73 ± 12^{ABb}	82 ± 13^{Aa}	72 ± 19^{A}	190 ± 133^{Bc}	463 ± 145^{BCa}	374 ± 184^{Ab}	343 ± 186^{A}
Herbicide + Mulch (H+M)	7 ± 7^{Db}	39 ± 17^{Da}	39 ± 27^{Ea}	28 ± 23^{B}	3 ± 1^{Fc}	66 ± 21^{Fb}	78 ± 31^{Fa}	49 ± 39^{B}
Herbicide + Microtopography (H+T)	2 ± 1^{Db}	48 ± 16^{Ca}	52 ± 14^{CDa}	34 ± 26^{B}	3 ± 1^{Fc}	73 ± 37^{Fb}	193 ± 165^{Ea}	90 ± 121^{B}
Mulch + Microtopography (M+T)	63 ± 14^{ABb}	81 ± 10^{Aa}	80 ± 25^{ABa}	74 ± 19^{A}	141 ± 145^{Dc}	470 ± 50^{Ba}	372 ± 178^{Ab}	327 ± 190^{A}
Herbicide + Mulch + Microtopography (H+M+T)	1 ± 19^{Db}	37 ± 14^{Da}	44 ± 32^{DEa}	27 ± 24^{B}	2 ± 54^{Fc}	92 ± 85^{Eb}	223 ± 230^{Da}	106 ± 148^{B}

Table 4. Analysis of variance table testing main effects (site and treatment) and interaction effect (treatment x site) on the response variable (canopy cover).

	Degrees of freedom	Sum of squares	Mean squared	F value	Pr(>F)
Treatment	7	48730	6961.4	17.3718	<0.001 ***
Site	2	21921	10961	27.3512	<0.001 ***
TreatmentxSite	14	5726	409	1.0206	0.44
Residuals	96	38470	400.7		

Table 5. Native vs. non-native canopy covers by treatment type (C: control; H: herbicide; M: mulch; T: microtopography).

	Canopy Cover (%)	
	Native	Non-native
C	0.7	59.0
H	2.9	32.0
M	1.9	74.0
T	0.5	73.0
H+M	2.9	25.0
H+T	0.6	33.0
M+T	0.4	74.0
H+M+T	0.5	27.0

Plant densities across all plots averaged 207±192 m^{-2} (data not shown) with controls averaging 297±177 m^{-2} and treatment means (based on midpoint ranges) between 49 and 355 m^{-2} (Table 3). When comparing means to the control and aggregating across sites, we see the same pattern in densities as we did in canopy covers. Treatments that included herbicide (H, H+M, H+T, and H+M+T) resulted in lower densities than treatments that did not include herbicide. H, H+M, H+T, and H+M+T densities did not differ from one another. Similarly, there were no differences between non-herbicide treatment densities M, T, and M+T and the control (Table 3).

Similar to native versus non-native canopy covers, densities were lower for native species than for non-native species (paired t-test: p<0.001; Table 7). The mean native species density for non-control treatments was 2±1 m^{-2}, or 80-fold lower than corresponding non-native species density of 205±135 m^{-2} (Table 7).

Table 6: Analysis of variance table testing main effects (treatment and site) and interaction effect (treatment x site) on plant density.

	Degrees of freedom	Sum of squares	Mean squared	F value	Pr(>F)
Treatment	7	1894830	270690	18.6987	<0.001***
Site	2	728184	364092	25.1507	<0.001***
Treatment: Site	14	383205	27372	1.8908	0.03669 *
Residuals	96	1389739	14476		

Table 7. Native vs. non-native densities by treatment type (C: control; H: herbicide; M: mulch; T: microtopography).

	Densities (m^{-2})	
	Native	Non-native
C	2.2	295.0
H	5.3	81.0
M	2.9	354.0
T	1.7	343.0
H+M	2.1	47.0
H+T	2.2	87.0
M+T	1.5	326.0
H+M+T	1.3	104.0

Site Patterns. Sites had a strong effect on canopy covers (p<0.001) and densities (p<0.001; Table 3, Table 4, Table 6). Both canopy covers and densities were lower at the CIN site than at either of the Reese Creek sites when considering all species, both native and non-native together (p<0.001; Table 3), while the Reese Creek sites were not different from one another (canopy cover p=0.885; density p=0.553).

Averaged across treatments, Reese Creek sites showed nearly double the total plant canopy covers (CIN=33±34%, RCN=59±23%, RCS=60±29%) and nearly triple the densities (CIN=88±146 m^{-2}, RCN=253±213 m^{-2}, RCS=240±170 m^{-2}) of the CIN site (data not shown). However, when considering native versus non-native species, CIN hosted greater canopy covers and densities of native species compared to Reese Creek sites, although canopy covers and densities of non-native species were much greater than those indices of native species (Figure 5). This trend was particularly evident between CIN and RCS (canopy cover p=0.01; density p=0.001).

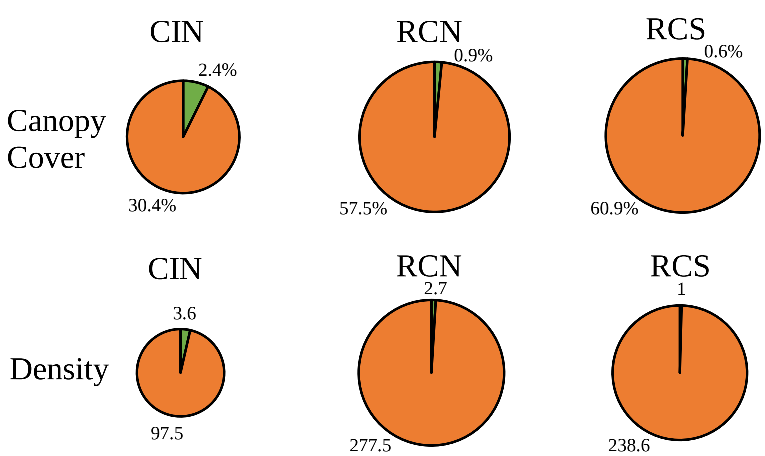


Figure 5. Native species (green) and non-native species (orange) canopy covers (%) and densities (m^{-2}) across sites. Pie chart areas were determined as relative canopy cover or density of one site compared to the others.

The plant community was dominated by a few species. Across all sites and treatments, the non-native, winter annual *A. desertorum* was the dominant plant of the 19 species identified: it was present in 106 of the 120 plots and its mean density (194±189 m^{-2}) was six times greater than that of any other species (Table 8). The canopy cover of *A. desertorum*, 36% (data not shown), was almost twice the cover of the second most abundant species, the non-native, summer annual *Salsola tragus* (Russian thistle). *Salsola tragus* was present in 81 of 120 plots with an average density of 34±25 m^{-2}. The standard deviation of the densities of these two plants highlights species abundance variance across sites. The density of *Salsola tragus* was around 3±24 m^{-2} at the RCN and RCS but only 0.1±0 m^{-2} at the CIN site. Another species, *Lappula squarrosa* (European stickseed) was most abundant at RCS, with even greater variability across and within sites (CIN= 0.03±0 m^{-2}, RCN= 4±8 m^{-2}, RCS= 21±17 m^{-2}).

We found nine native species in this study. Five of those species were seeded (*E. trachycaulus*, *P. secunda*, *P. spicata*, *A. millefolium*, *A. frigida*). No individuals of the seeded *H. comata* survived to maturation. The remaining four native species found in this study were volunteers (*Solanum triflorum* Nutt. [Wild tomato], *Oenothera biennis* [Common evening-primrose], *Cleome serrulata* [Rocky Mountain bee plant], *Oryzopsis hymenoides* [Indian ricegrass]). *Elymus trachycaulus* was the most abundant of the seeded native species, occurring in 51 of 120 plots with a mean plant density of 3.2±3 m^{-2}. Though *P. spicata* occurred in only 15 of 120 plots, when present, it was the densest native species at 3.8±4 m^{-2}, though this density was still nearly an order of magnitude lower than the density of *S. tragus* and 50-fold lower than the density of *A. desertorum* (Table 8).

Densities are presented here both as a mean for plots in which the species was present, as well as the total mean in all plots. Both are presented to showcase the heterogeneity of results. Cheatgrass, for example, was only found in eight plots, but had a mean density of 15±27 m^{-2} (CV>100). Showing only the total mean leads us to believe that cheatgrass management is unimportant; given the potential for an exponential expansion, however, management might be valuable before cheatgrass spreads beyond a small subset of plots (Table 8).

Table 8. Species densities (m^{-2}) for all 19 species found in the Gardiner Basin study, and their status as native (N) or non-native (NN). Statistics (means, standard deviations [SD], and coefficients of variation [CV]) were calculated using only the number of plots where species were observed (a) or all 120 plots (b).

Common Name	**Latin Name**	**N or NN**	**Observed in # of plots**	**a. Densities calculated using only plots where present**			**b. Densities calculated using all 120 plots**		
				Mean (m^{-2})	SD (n variable)	CV (%)	Mean (m^{-2})	SD (n=120)	CV (%)
Desert alyssum	*Alyssum desertorum*	NN	106	194	189	97	172	2	1
Russian thistle	*Salsola tragus*	NN	81	34	25	74	23	3	11
European stickseed	*Lappula squarrosa*	NN	56	18	17	96	8	8	91
Cheatgrass	*Bromus tectorum*	NN	8	15	27	>100	1	<1	57
Annual wheatgrass	*Eremopyrum triticeum*	NN	12	7	10	>100	<1	<1	>100
Bluebunch wheatgrass	*Pseudoroegneria spicata*	N	15	4	4	92	<1	<1	19
Slender wheatgrass	*Elymus trachycaulus*	N	51	3	3	93	1	<1	7
Wild tomato	*Solanum triflorum Nutt.*	N	3	3	2	78	<1	<1	>100
Tumble mustard	*Sisymbrium altissimum*	NN	9	2	1	71	<1	15	>100
Fringed sagebrush	*Artemisia frigida*	N	6	2	2	87	<1	<1	>100
Western yarrow	*Achillea millefolium*	N	7	2	1	65	<1	<1	>100
Crested wheatgrass	*Agropyron cristatum*	NN	7	1	1	55	<1	<1	>100
Indian ricegrass	*Oryzopsis hymenoides*	N	19	1	1	56	<1	<1	72
Rocky Mountain beeplant	*Cleome serrulata*	N	5	1	1	39	<1	<1	>100
Common evening-primrose	*Oenothera biennis*	N	1	1	*NA*	*NA*	<1	<1	>100
Field pennycress	*Thlaspi arvense*	NN	1	1	*NA*	*NA*	<1	188	>100
Prickly lettuce	*Lactuca serriola*	NN	2	1	0	0	<1	26	>100
Sandberg bluegrass	*Poa secunda*	N	3	1	0	0	<1	<1	>100
Western salsify	*Tragopogon dubius*	NN	7	1	0	0	<1	4	>100

Interaction Patterns. Canopy cover was different both across sites and with restoration treatments (Table 4), but there was not a treatment x site interaction effect. The plant densities (Table 6) showed significant main effects (ANOVAs, $p<0.001$ for both main effects) as well as the interaction term (ANOVA, $p=0.04$). Plant densities were influenced by treatments, by sites, and by the interaction of treatment and site (Table 6).

Considering the four herbicide treatments at CIN (H, H+M, H+T, H+M+T), where canopy cover was reduced from 40% in the control to 1-7%, herbicide was very effective at bringing canopy cover close to 0% (Table 3). The same application of herbicide at the Reese Creek sites, by contrast, only reduced cover from 69% (control) to 37-53%, a more modest effect (Table 3).

Topographic Patterns. Canopy cover in the micro-highs (0.5 m^2) and micro-lows (0.5 m^2) of the microtopographic treatments were compared to one another and against the control as a reference (combined across sites; Figure 6). Micro-high and micro-low canopy covers are significantly different from one another (paired t-test, $p=0.002$; Figure 6). Micro-lows also significantly differed from controls (paired t-test, $p<0.001$). Averaged across all three sites, the mean canopy cover was reduced from 60% (SD=33) in the control plots to 30% (SD=19) in micro-lows and to 22% (SD=17) in micro-highs (data not shown).

At the CIN site, canopy covers in micro-lows without herbicide were slightly greater than those of controls, but canopy covers in micro-highs without herbicide were slightly less than those of controls (Figure 6a), although the variability at control plots was greater than for any other site and/or treatment. At the Reese Creek sites, control canopy covers were greater than those of both micro-lows and micro-highs, and micro-low canopy covers were greater than micro-high canopy covers, with the single exception of H+M+T at RCS.

Microtopography at the treatment level did not lead to large differences. There were a few differences in means, like M+T at Cinnabar (+23.8% higher in the micro-lows), T at Cinnabar, (+18.2% higher in the micro-lows), and H+T at Reese Creek South (+20.2% higher in the micro-lows (Figure 6).

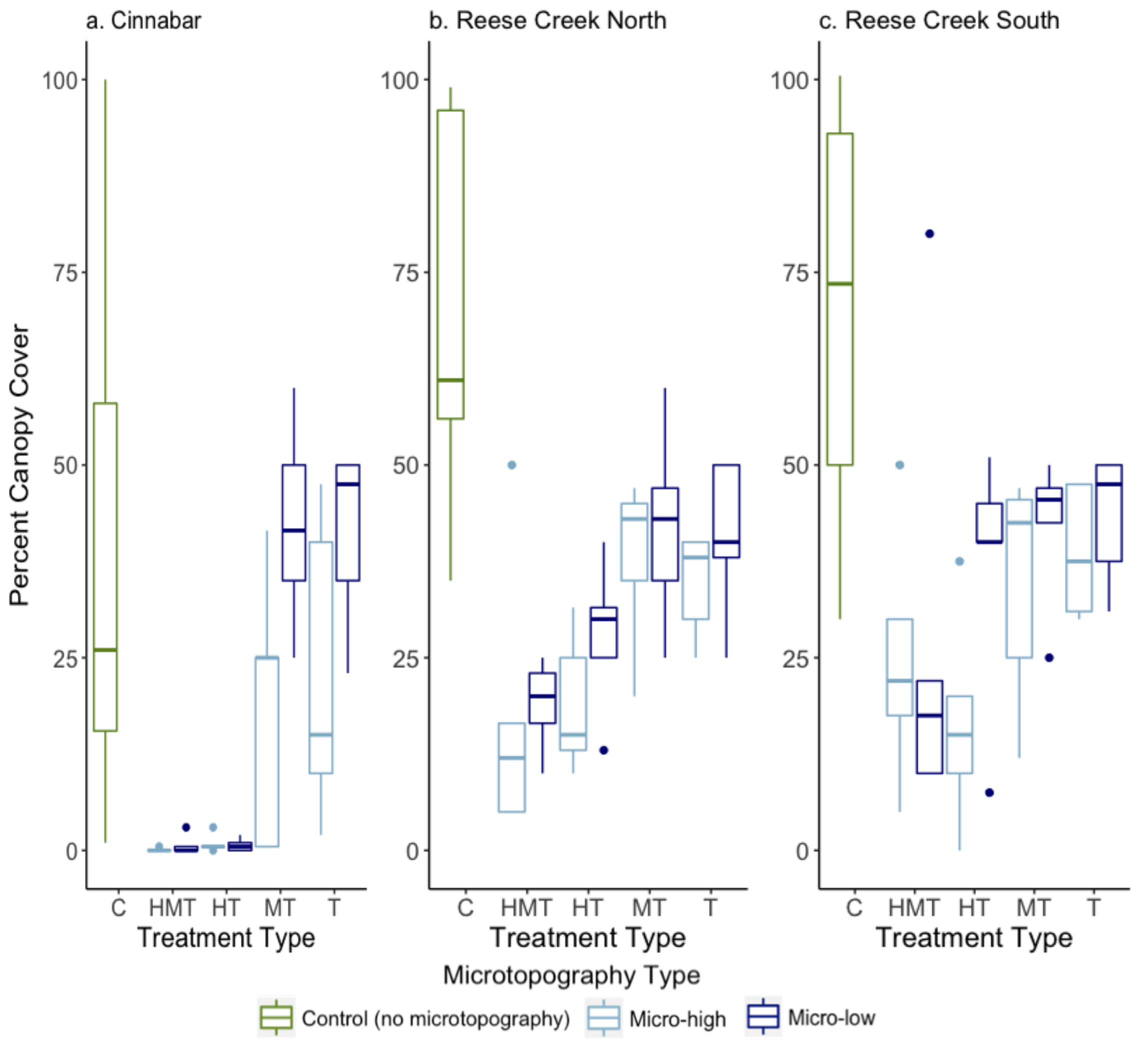


Figure 6. Microtopographic effects on canopy cover expressed as box plots; microtopography is separated into micro-highs and micro-lows, and results are presented singly (T) or in combination with herbicide (H) and/or mulch (M) relative to controls (C). Sites: a. Cinnabar; b. Reese Creek North; c. Reese Creek South.

Soil moisture sensors revealed broadly consistent patterns across the three sites, with values ranging across an order-of-magnitude from about 3% (0.03 m^3 moisture per m^3 soil) in late summer to nearly 30% in late spring and early fall (Figure 7). Micro-lows did not show greater volumetric water content relative to either paired micro-highs or paired control treatments (Figure 7). For example, micro-low soil moisture levels at CIN were higher than both the corresponding micro-high plot and the control plot in spring 2017, but by late fall micro-low soil moistures were lower than micro-high soil moistures, both of which were still greater than the control (Figure 7d). As another example, at RCN, micro-low or micro-high soil moistures in plots amended with mulch were generally lower than soil moisture in the mulch-only plot, which served as a “control” for this site (Figure 7e). Finally, at RCS, both micro-low and micro-high soil moistures in plots amended with mulch were initially lower than the control plot before increasing in late May (Figure 7f).

Our data show a season-microtopography interaction, with early-growing-season (before July 1) soil moistures in micro-lows being up to 5% (on an absolute basis) greater than corresponding soil moistures in micro-highs, but late-growing-season (after October 1) soil moistures in micro-highs being up to 8% greater than corresponding soil moistures in micro-lows (Figure 7a, d). At CIN, cumulative delta values were both positive relative to the corresponding control plot and differed seasonally but not on an absolute basis (micro-high: 0.036, micro-low: 0.037; two sample t-test, $p=0.69$).

At RCN where the micro-highs and micro-lows were normalized against mulch as a “control,” the micro-low had the smallest mean delta value of all sites and treatments. In other words, at this site, micro-lows and mulch were most similar in their effects on volumetric water content (Figure 7e).

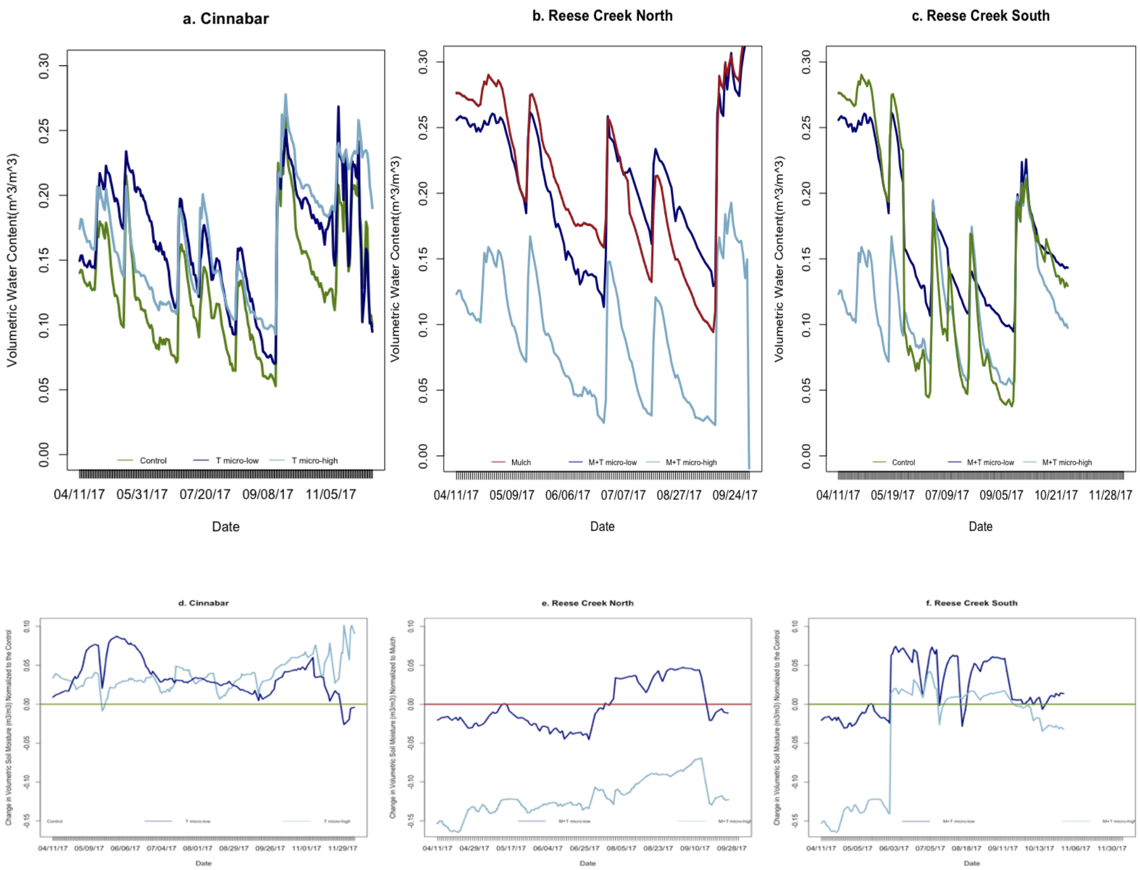


Figure 7. Growing season volumetric soil moisture (m^3m^{-3}) at a. Cinnabar, b. Reese Creek North, and c. Reese Creek South from April 11, 2017 to fall or winter 2017. Corresponding figures d, e, and f show volumetric soil moisture differences for micro-low (dark blue lines) or micro-high (light blue lines) plots normalized to corresponding control (CIN, RCS; green lines) or mulch plots (RCN; brown line) for post-precipitation wet-up events.

Discussion

Research findings on cost-effective restoration techniques have broad management implications that, if successful, can be scaled across 200 hectares in the Gardiner Basin and perhaps across millions of hectares under threat in semi-arid regions by invasive species.

Overall, our study showed very low establishment of native species, particularly when compared non-native species abundance. Fewer than 300 of ~520,000 seeds survived to maturation at the time we sampled in the first growing season after seeding. However, immediate plant recruitment may be stalled by seeds' adaptations to remain dormant in the soil until a site receives sufficient precipitation (Flores & Jurado, 2003). Seed bank dynamics and plantings do not always lead to success if conditions are not favorable (Fick et al., 2016); instead, longitudinal studies to monitor species germination and maturation over multiple growing seasons are necessary. While it is possible some additional seeds might have germinated and survived to maturation through the second growing season, the experiment was terminated after only the first growing season due to accidental mechanical and chemical disturbance. Low native seedling establishment was predicted by the National Park Service at the start of their project due to low annual precipitation, high winds (Appendix A, Figure A9; DOI: 10.5281/zenodo.1213337), and competition with non-native plants (Interagency Workshop Steering Committee, 2005).

Unsurprisingly, herbicide decreased the presence of winter annuals due to the timing of spraying, which targeted the most widespread of the species, *A. desertorum*, during its overwintered seedling stage. Compared to native, perennial grasses which grow and go dormant once per year, *A. desertorum* is able to undergo up to four flushes of seedlings maturing and emerging in a calendar year (S. Dillard, pers. obs.); in certain settings, *A. desertorum* is both a winter annual and a summer annual species. Only following herbicide treatment might native plants establish in higher numbers and preferentially colonize the early-season moisture-storing micro-lows, though we only observed mean cover values as high as 20% for combinations of H and T (Figure 6), and across all three sites the non-native H+M+T plant cover was 54-fold greater than native cover (Table 7).

Herbicide can be a very useful tool, but any advantages must be weighed against potential disadvantages. For example, only herbicides with low soil residual have been used by the National Park Service, in part due to the restoration site's location immediately adjacent to the Yellowstone River. The bond that the herbicide forms with the soil must also be considered when determining whether the chemicals are mobile. If they are, herbicides have the potential to compromise the critical habitat this river corridor represents for the declining endemic Yellowstone Cutthroat Trout (Battaglin et al., 2003; Lee et al., 2002; Scribner et al., 2003). Furthermore, long-term herbicide applications that successfully eradicate non-native species can create large-scale vacant niches, both in terms of the size of the niche and how much of the ecosystem is bare, which can increase the rate of wind and water soil erosion. Thus, successful herbicide applications could inadvertently promote increased sedimentation of the Yellowstone River from both wind and water erosion (Appendix A, Figure A9; DOI: 10.5281/zenodo.1213337) of the adjacent restoration sites; increased sedimentation can, in turn, smother fish eggs and lead to population declines (Erman & Ligon, 1988; Turnpenny & Williams, 1980; Wood & Armitage, 1997). Thus, from an ecosystem management perspective, the potential erosion-control benefits of high non-native species canopy cover could outweigh the erosive damage of low native species canopy cover. In this specific scenario, managers may have the unenviable task of deciding whether restoring native plant species on ~20 hectares of the pilot revegetation project is of a higher priority than protecting the Yellowstone Cutthroat Trout from increased sediment supply from those corresponding ~2.5 river kilometers. If sprayed with herbicide, resulting vacant niches should be seeded with desirable plant species, and quickly, to optimize both on-site and off-site outcomes. Quick revegetation at this site is limited by drought and high wind, though, and colonization of desirable species is likely to take years. Under any current scenario, native ungulates for whom the Gardiner Basin restoration project was originally started are not foraging adequately in the Gardiner Basin (Zavaleta et al., 2001).

In the absence of herbicide, both plant canopy cover and density were elevated in micro-lows. Plants seemed to preferentially grow here (Figure 6), validating their status as nurse sites, although non-native species made up a majority of micro-low canopy covers and densities. Non-native species dominance could be explained by spade-induced microtopography turning over the seed bank and exposing dormant non-native seeds that were once buried. Ruderal species, which are often annuals subject to persistent and severe disturbance, are characterized by high propagule pressures (Grime, 1977). For example, *A. desertorum* may have as many as 9 seeds cm^{-2} (Hamilton, 2014) which, when scaled, amounts to 90,000 seeds m^{-2}. Compared to a study of fine-textured grasslands in Colorado where perennial grass seed was found at a rate of 355 seeds m^{-2} pre-growing season to 68 seeds m^{-2} in mid-growing season (Coffin & Lauenroth, 1989), annual species like *A. desertorum* appear capable of overwhelming native plant seeds. After drought, there is evidence that winter annual grasses-- analogs to *A. desertorum* in this system-- accumulate in the seed bank, while perennial grass densities remain low (Hild et al., 2001). Coupled with vacant niches, high propagule pressure may keep non-native species, whether forbs or grasses, dominant in the system. The threat of non-native dominance and persistence may provide an argument for targeted pre-emergent herbicides to address heavy seed rain or a high seed bank density.

At both Reese Creek sites, located on a lower river terrace close to the Yellowstone River, microtopography had less of a positive impact on plant cover and densities than at CIN, which was located on an upper (older) river terrace. The soils at the Reese Creek sites are characterized by better drainage than the CIN site, consistent with their younger geomorphologic/pedological status (Hellquist et al., 2011). This improved drainage at the Reese Creek sites may have lessened the effects of microtopography on plant canopy cover and densities relative to the CIN site. At the Reese Creek sites, in fact, a comparison of matched micro-low treatments (H+T, H+M+T) showed nearly twice the total density (native + non-native species) as corresponding treatments at CIN, which could be related to higher soil moisture (Table 3; Appendix B, B3; DOI: 10.5281/zenodo.1213337).

At CIN, only eight species were identified, while at the Reese Creek Sites, 19 species were identified, indicating a difference in plant community composition. The difference in plant canopy covers and densities between the sites can be explained in part by the presence of *S. tragus,* which, of the 19 species identified, was the third least abundant species at CIN but was the second most abundant species after *A. desertorum* at both RCN and RCS (data not shown). *Salsola tragus* is a larger-statured summer annual with a maximum height of 1.2 m, while *A. desertorum* only reaches a maximum height of about 20 cm at this site (U.S. Department of Agriculture, Natural Resources Conservation District, 2018). Although not the most abundant species in terms of individuals per unit area, *S. tragus* was the largest species censused. The Reese Creek sites support a more diverse (albeit non-native) and a larger-statured plant community than CIN.

Overall, the plant community was dominated by only a few species. The Gardiner Basin is not a highly diverse area in terms of vegetation; in fact, of 19 total species recorded, four species-- natives *P. secunda* and *O. biennis* and non-natives *Lactuca serriola* (prickly lettuce) and *Thlaspi arvense* (field pennycress) were present with fewer than five individuals across all plots and sites. Conversely, over 20,000 *A. desertorum* individuals were counted across all plots and sites (data not shown), which is likely an underestimate due to sampling procedures using bins. In fact, *A. desertorum* was present in densities >500 in 14 of the 106 plots on which it occurred. The diversity, density, and dominance of non-native species in the Gardiner Basin is widespread.

Microtopography alters soil moisture conditions, which could exert an abiotic filter on seed germination and plant establishment. Micro-lows did collect a greater volume of precipitation, particularly during the early growing season. This was shown by a greater volumetric soil water content in micro-lows compared to micro-highs or controls in the early growing season except at Reese Creek South (Figure 7). We cannot be sure if seed germination rates or seedling phenology was altered by these differences in soil moisture (amount as well as timing of plant-available-water), but we did observe micro-lows filled with ice in late winter and early spring when unmanipulated ground and adjacent control plots were bare (Appendix A, Figure A1; DOI: 10.5281/zenodo.1213337).

The mechanisms by which mulch interacts with microtopography and site to invert the expected moisture level differences between micro-lows and micro-highs are unknown. This pattern warrants further study to inform our ecological understanding of how these specific types of treatments might be combined to improve restoration outcomes as well as the robustness of these findings, especially since these patterns are drawn from a spatially limited experiment.

As the risk of more intense and prolonged droughts threatens ongoing restoration projects across this region (Harris et al., 2006; Whitlock et al., 2017), microtopography as a restoration tool is worth more attention and research. Tractor machinery such as a discer or a Dammer-Diker® bar can quickly and cost-effectively implement microtopography on a larger scale, making this technique accessible to semi-arid restoration projects beyond the Gardiner Basin. Especially coupled with other restoration techniques that help prepare a site for restoration like non-native species control and surface mulching, microtopography can help ameliorate relatively harsh site conditions slightly less prohibitive to restoration success.

Conclusions

At the treatment level, our study showed plant canopy cover and density were most affected by herbicide application, either singly or in combination. Mulch treatments (singly or in combination with H and T) generally failed to boost native plant cover and densities. Microtopography did boost canopy cover and number of individuals, but the majority was non-native. If non-native species were under control in the Gardiner Basin, we suspect we would see larger treatment effects between soil surface treatments like mulch and microtopography. Sites also differed from one another with the two Reese Creek sites on the lower river terrace being more similar than the CIN site on the upper river terrace. We also know that the plant communities are different at the three sites. Perhaps most importantly, our study showed that in the first year after seeding, reduced competition with non-native plants (*i.e.*, reduced canopy covers and densities) did not encourage native plant growth. This implies that, in order for native plants to establish in the Gardiner Basin, managers must find a way to improve environmental conditions at the site instead of prioritizing eradicating non-native species. These patterns can help managers effectively plan restoration treatments to target desired outcomes on different sites. Future research should reaffirm the opportunities this historic and ecologically significant corner of the world represents.

CHAPTER THREE

FUTURE DIRECTIONS

This study had a robust, multi-treatment experimental design with five replicates at each of the three sites. We discerned differences in canopy covers and densities between seven treatments and a control, and soil moisture differences between nine treatments and a control across the Gardiner Basin of Yellowstone National Park to inform land managers about potential restoration techniques. Our results from the effects of each of the three treatments, (herbicide, mulch, and microtopography) imply tradeoffs as well as possible cost savings. For example, though herbicide reduced plant cover and plant densities, this could also have increased the site's susceptibility to accelerated wind soil erosion. As another example, microtopography increased plant cover and plant densities, but those increases were largely made up of non-native species which then must be controlled through cost- and/or labor-intensive methods like spraying herbicides or hand-pulling.

Study Limitations

This study was designed to assess restoration techniques that may be of use to land managers in the Gardiner Basin and at other sites dominated by non-native species in semi-arid ecosystems. Of course, implementing treatments on small (square meter) plots is much simpler than on a large scale like the ~20-hectare National Park Service revegetation project, though it also allowed for replication. However, small plots may not have been representative of the broader revegetation site. Measuring the effect of microtopography on small plots could have provided different results than if it had been implemented, say, on 10 or on 100 m^2 plots. Propagule pressure from the surrounding untreated areas could have disproportionally affected the small plots as these often can exhibit edge effects. If plots had been larger, edge effects from unmanipulated areas would be less likely. Restrictions in our National Park Service research permit required small plots, in part to minimize the area of land taken out of circulation for the broader revegetation efforts.

Little has been published about *A. desertorum*, and basic tests on germination and seed production remain unknown. *Alyssum desertorum* has become more widespread across the semi-arid West in recent years, and these types of analyses, as well as improved characterization of its allelopathic potential, could improve our understanding of its invasive traits. The Gardiner Basin is the only documented case of monoculture-like dominance of desert alyssum in a somewhat natural, though disturbed, non-native setting. In addition, other species of *Alyssum* (Brassicaceae) are known to hyperaccumulate metals in other semi-arid regions, like the serpentine soils of California (Broadhurst & Chaney, 2016). We do not yet know if *A. desertorum* shares this adaptation, but this information might help explain its spread through other areas of the Greater Yellowstone Ecosystem (Rew et al., 2004), a heavily mineralized zone with the highest global density of terrestrial geothermal features. We also do not know if soils in the Gardiner Basin contain elevated levels of heavy metals. We cannot infer *A. desertorum's* dominance to the presence of heavy metals, but this potential association, or lack of association, could be helpful to managers in the future.

As with all research, funding was a limitation of this study. We were funded by two small grants totaling $1,800 from the Montana Academy of Sciences and the Montana Institute on Ecosystems. With additional funding, more soil moisture sensors would have been deployed across treatments to assess the impacts of herbicide, mulch and microtopography on soil water dynamics. Higher quality soil moisture sensors also may have helped reduce variability, although without testing our Hobo data loggers against higher quality loggers, we do not know if the variability is due to the loggers or simply due to environmental characteristics. Additional funding would have also allowed for a greenhouse study to understand native and non-native species' drought thresholds as well as any impacts that combinations of non-native species may have on native species. Numerous studies detail the impacts of single non-native plants, but the literature lacks combination effects of multiple non-native species on a native plant community. There is still potential to fill this research gap in the future, and *A. desertorum* seeds have been wild-collected in case funding becomes available for follow up research.

The main limitation of this study was time. Trying to measure restoration success in a field study context on the time scale of one to two years is challenging under any circumstances, although not uncommon. Longer-term monitoring is necessary to validate treatment effects against potential confounding environmental variables. Further complicating a short monitoring period, accidental chemical and mechanical disturbance from the National Park Service was observed on about half of the study's 120 plots after plot establishment and before measuring response variables. Although both disturbance types could have affected study results, our frequent monitoring of the site suggest these effects were minimal prior to the 2017 surveys.

Extrapolating Treatments to a Large Scale

Herbicide

A diversity of herbicides—pre- or post- emergent, no residual to high residual, and non-discriminatory or broadleaf—can be used to prepare a site for restoration. In this study, post-emergent, low residual, non-discriminatory herbicide was applied with a backpack sprayer, which is tedious for non-native plant control on a large-scale. To extrapolate herbicide use to large revegetation areas, herbicide can be hand sprayed from off-road vehicles or even aerially sprayed from a small aircraft. The National Park Service uses both of these methods within the Greater Yellowstone Ecosystem. Off-road vehicles have been used at the revegetation project in Gardiner, MT (Renkin, 2014), and aerial spraying was recently included in the 2018 budget for Grand Teton National Park (Klaptosky, pers. comm.).

Pros and Cons of Herbicide Use. In the National Park Service, preservation is the first priority. Often times, preservation requires the removal of non-native species, notably if they are noxious weeds. The benefits of herbicide for easily controlling large areas dominated by non-native plants must be weighed against the consequences. Depending on the type of herbicide, residuals in the soil may contaminate nearby sites via erosion including groundwater (Blanchard & Donald, 1997; Guzzella et al., 2006) or surface water (Gruessner & Watzin, 1995). Herbicide may also impact soil biota (Greaves et al., 1976; Roper & Gupta, 1995). In the case of the Gardiner Basin, herbicide has been applied as many as four times in a calendar year, and high winds are common (Renkin, 2014; Appendix A, Figure A9, DOI: 10.5281/zenodo.1213337). Between spraying herbicide, usually in the fall, and native plant emergence in the spring, standing dead aboveground biomass created by herbicide use is not sufficient to prevent widespread wind and water erosion. The loss of the upper few millimeters or even centimeters of organic matter-rich soil to wind and water erosion may be more damaging to restoration success than non-native species that hold soil in place. In the Gardiner Basin, changing the timing of herbicide application from the fall to the late winter or early spring to kill winter annual plants without affecting native perennial grasses may reduce the amount of soil lost to erosion.

Mulch

Soil surface cover can reduce soil water evaporation, which is perhaps the most important benefit that mulch can offer in a semi-arid landscape (Groenevelt et al., 1989; Ji & Unger, 2001). In this study, bulk red cedar mulch was hand-spread, which is too labor intensive for a large-scale project. Efficient agronomic methods for spreading amendments can use a mulch spreader behind a tractor.

Pros and Cons of Mulch Use. Mulch comes in many forms. It can be a synthetic substance, sometimes made from recycled materials like rubber tires. Mulches can also be organic with varying carbon: nitrogen ratios (C:N), like hay with a low C:N, or bark chips with a high C:N. In semi-arid regions with low decomposition rates, woody materials decompose slowly and may immobilize nitrogen (Cione et al., 2002; Reever Morghan & Seastedt, 1999). Reever Morghan & Steastedt (1999) found that wood materials may decrease native grass densities, especially in the presence of non-native seed rain which is widespread in the Gardiner Basin. This suggests that if mulch is used as a restoration treatment, it should be in combination with other follow-up restoration treatments. Other surface cover materials such as straw, hay, coconut husk, or sheep wool products have lower carbon to nitrogen ratios and so may more quickly contribute mineralizable nutrients to the soil. However, in an area subject to high winds like the Gardiner Basin, the longevity of lighter materials is questionable. Straw and hay could also inadvertently attract grazers in unfenced restoration areas.

Microtopography

The micro-lows and micro-highs increased volumetric soil water above that of a control plot. The micro-lows were hand-dug, and the displaced soil was used to make the micro-highs. Extrapolating this treatment to a large-scale requires a tractor and a specialized attachment like a Dammer Diker®.

Pros and Cons of Microtopography Use. The water-related and soil preparation benefits may be worth the disturbance created by microtopography. Microtopography reduces the bulk density of the soil by loosening the upper horizon and turning it over, which can increase soil water infiltration. Conversely, implementing microtopography without plant establishment could lead to soil organic matter loss via erosion. In addition, disturbing the soil surface initially turns over the seed bank, which, if contaminated with non-native species seed, could result in an initial non-native species flush. Non-native species control is almost certainly required with microtopography implementation in this type of setting. Additional research should be done defining tradeoffs between the resources required to create microtopography at different scales, different height to width ratios, and the longevity of the types of features in the Gardiner Basin's windy setting.

Cost Analysis

The three treatments assessed in this study have varying costs. The costs presented here do not include the costs of labor or additional equipment.

Herbicide is usually bought in concentrate and mixed with water to site-specific rates. Herbicide costs vary widely based on the brand and length of residual. For this study, we used Roundup® concentrate, diluted at 1.5%, a rate common for controlling annual invasive species. To treat the ~20-hectare restoration project with 1.5% Roundup®, herbicide costs would total about $1,000, assuming applicator equipment and operators are available. Treating the entire ~300 hectare of the Gardiner Basin would cost about $15,000 in materials. These costs are per treatment; herbicide can become very costly if multiple treatments are needed per year.

Covering tens or even hundreds of hectares with mulch is prohibitively costly. Estimates for 3 centimeters depth of mulch, as was used in this study, across a ~20-hectare restoration project equal ~ $400,000, and for the ~300-hectare Gardiner Basin, almost $6 million. In a National Park, any surface cover materials must be certified weed-free, which may additionally increase the cost of materials. Woody products are generally not contaminated with seed of any kind, native or non-native, but straw or hay is quite commonly contaminated. Other restoration projects have used cost-saving strategies for producing mulch like chipping their own from city yard waste and holiday tree dump sites. This is a good option for small restoration projects or projects near medium- to large-sized cities, but a small, rural town like Gardiner cannot possibly produce enough yard waste to cover the ~20-hectare revegetation sites, or the ~300 hectares of the Gardiner Basin in need of restoration. In combination with other restoration treatments, mulch could be used sparingly in problem areas to minimize cost and labor.

Installing microtopography requires specialized tractor equipment like a Dammer Diker®. A Dammer Diker® can be purchased used for about $8,000 and new for about $30,000. Similar equipment may be rented at daily rates if available in the area. Of the three restoration treatments, microtopography requires only one treatment and has no maintenance costs, so is likely the cheapest in the long term. The National Park Service already owns the tractor necessary to implement this treatment, but if they didn't, tractors can also be rented at daily rate.

Restoration is costly, but if planned well and implemented correctly, only needs to be done one time. The National Park Service project in the Gardiner Basin, as of 2014, cost over $1 million. A majority of those costs (over $900,000) went to seed contracts with Bridger Plant Materials Center, to staff salaries, and to the fence contract to enclose ~20 hectares (Renkin, 2014). The National Park Service revegetation plan was based on suggestions from agency, industry, and academic professionals, and these recommendations are likely broadly applicable to other disturbed sites in semi-arid regions (Interagency Workshop Steering Committee, 2005). The challenges are unique at every restoration site, but the concepts gleaned from our study of herbicide, mulch, and microtopography may also broadly apply across semi-arid regions.

Figure 8 incorporates suggestions from the National Park Service revegetation project with our study results to form a conceptual model for restoration techniques in semi-arid regions based on common disturbance types. Here, we focus on site preparation, planting, and non-native species control post- wildfire, grazing, drought, or flooding. As we learned from the plant community and soil water differences between the Reese Creek and Cinnabar sites, the level of soil water moisture can drastically affect the plant community. Knowing this, we designed this conceptual model for maximum soil water storage depending on the disturbance type.

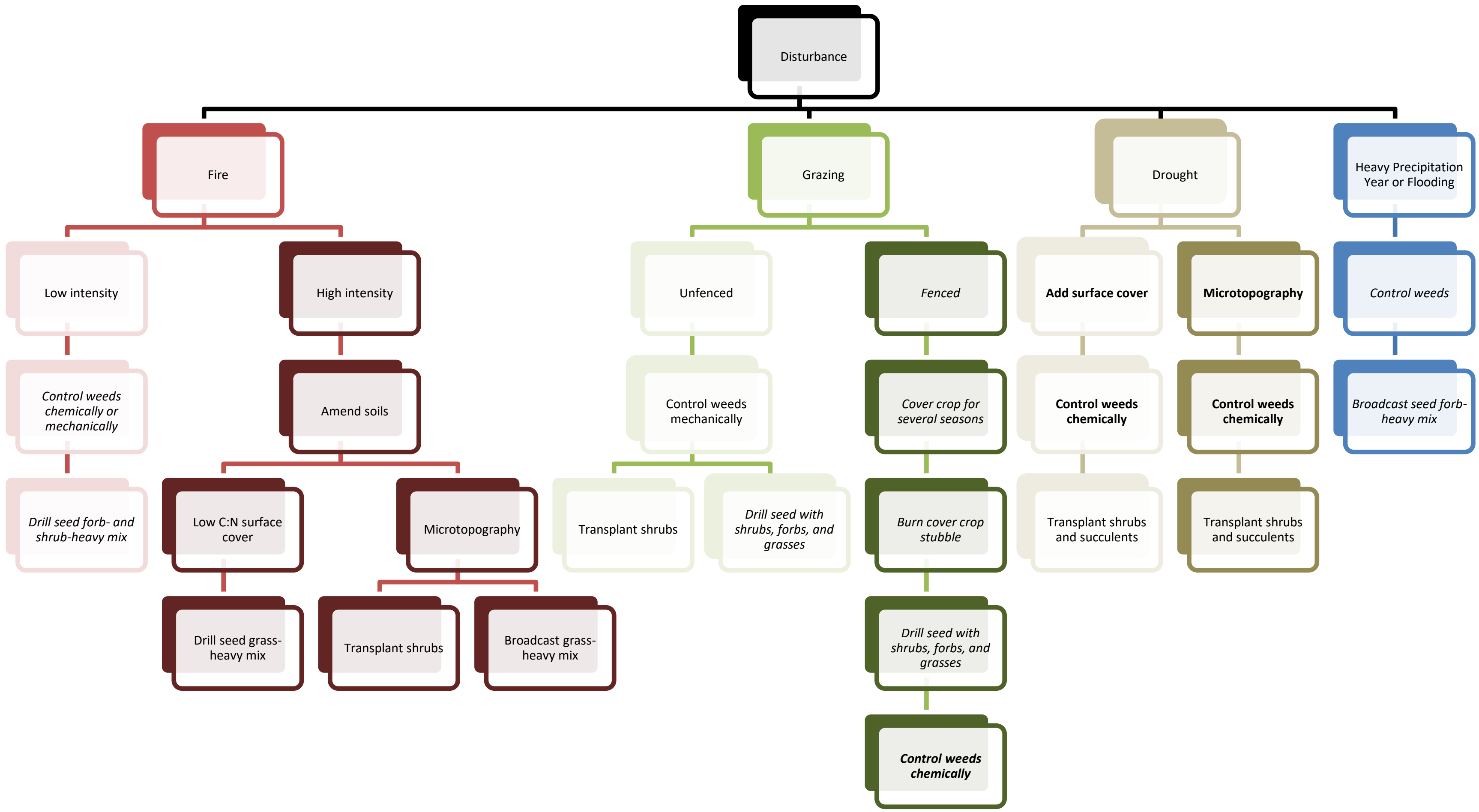


Figure 8. Conceptual model for non-native species control in a semi-arid restoration setting based on disturbance type. Bolded boxes are restoration treatments that were used in this study after the appropriate disturbance, while italicized boxes are ones from the National Park Service revegetation project.

Under increased disturbances like fire, grazing, drought and/or aridity, and flooding, this site could face severe problems eradicating non-native plants. Even if non-native plants were controlled via disturbance, the seed rain is rife with non-native species. More than 15 years ago, over 15% of all surveyed species in Yellowstone National Park were non-native (Whipple, 2001). The impacts of ~125 years of intensive degradation are quite evident and could almost certainly worsen if the site were exposed to one or more of these major types of disturbances.

Interactions between Treatments

The interactions we observed between our treatments give us hope, though, that this site still has the potential to return to a functioning grassland. We saw a few general trends in our data: treatments of mulch alone, microtopography alone, and mulch + micrography often produced similar results to the control, suggesting that chemical weed control is necessary at this site. Similarly, herbicide alone, herbicide + mulch, herbicide + microtopography, and herbicide + mulch + microtopography produced generally similar data. Herbicide was the single treatment that had the largest effect. The micro-lows within the soil surface variation, when coupled with herbicide, reduced the non-native species to native species canopy cover ratio by about half. Prolonged weed control, coupled with microtopography, which according to our cost analysis is preferable to mulch on a large-scale, is one potential solution to lessening the consequences of a major disturbance.

The Gardiner Basin was our natural laboratory for this study. This site is highly visible from the highway leading to the Roosevelt Arch at the Gardiner entrance, which attracted over 360,000 visitors to Yellowstone National Park in 2017 (Yellowstone National Park, 2018). Such a site that is highly visible, beloved by the American public, and of great ecological importance deserves further study to refine restoration strategies that are economically and ecologically feasible, and to build on the collaboration between the National Park Service and Montana State University.

APPENDIX

APPENDIX A

PHOTOGRAPHS

Figure A1. Six micro-lows implemented in 2016 retaining a snowpack later than surrounding micro-highs in 2018.

Figure A2. Cinnabar, Montana, in 1901. Disturbance from human settlement and the railroad created vacant niches and invited non-native species colonization (Yellowstone National Park, 2018)

PLATE: 2

LOCATION: View southwest to Electric Peak from Gardiner-Reese Creek road (520.7 E., 4987.2 N; elev. 1620 m)

PHOTOGRAPHERS: Ca. 1893 - Photographer unknown (NPS-YNP)
17 June 1971 -D.B. Houston
12 August 1990 - D.B. Houston

INTERVAL: Approximately 78 and 97 years. Camera points similar.

VEGETATION CHANGES:

Foreground substrate is a mudflow with clay soils. By 1990 there had been some decrease in greasewood, but vegetation in the swale was still primarily greasewood with scattered big sagebrush, bluegrasses, cheatgrass, and foxtail barley. Vegetation on the slopes is dominated by Sandberg's bluegrass and junegrass, with scattered bluebunch wheatgrass and phlox. A decline in shrubs, probably big sagebrush, occurred. An increase in grass cover occurred by 1971, but annual variations in the cover of grasses are spectacular at this low elevation. The 1990 retake was taken later in the summer, hence the vegetation was cured and the standing crop of grasses was greater. The site receives intensive grazing by native ungulates in winter. This area did not burn in 1988.

Background shows an increase in Douglas-fir on the lower slopes.

NOTES OF INTEREST:

This represents our earliest photo of vegetation in the boundary line area of the park near Gardiner, Montana. It is a very complex site. The appearance of the vegetation and soil surface in the original suggests that the bentonite clay soils (note the "pavement" of small stones on the soil surface) have low potential for supporting vegetation. Accounts of early travelers reinforce this interpretation. Military explorer Lieutenant Gustavus Doane of the U.S. Army (Bonney and Bonney 1970:236) described the general area in August 1870 as "passing from a dead level alkali plain to a succession of plateaus covered with a sterile soil,"--almost certainly a reference to the mudflow shown here.

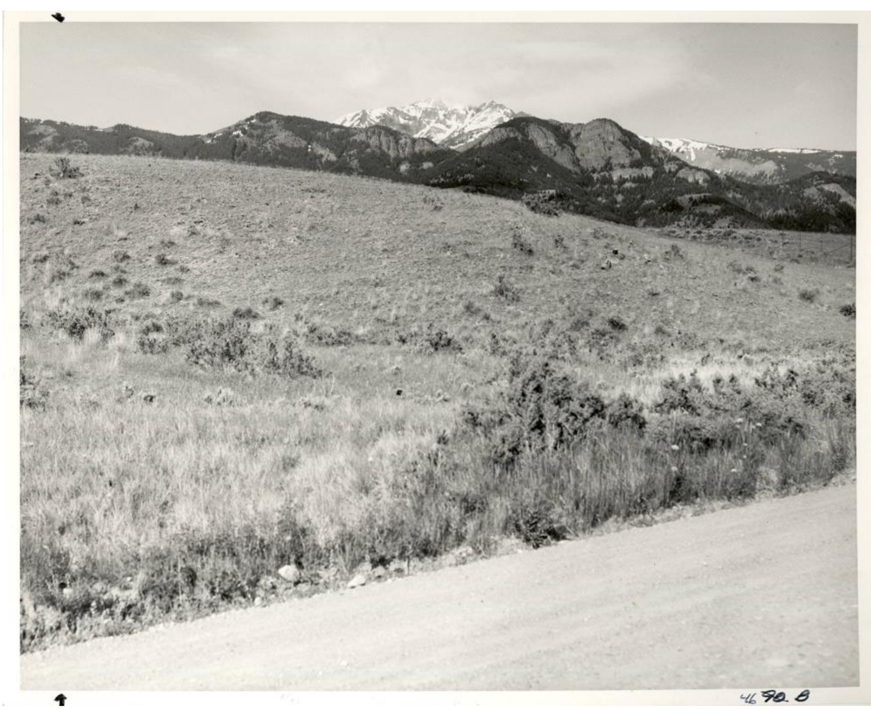
Terraces in the retake, and other information on human occupancy, suggest that intensive livestock grazing occurred year-round from the 1870's until the area was added to the park in 1932. The vegetation is also intensively utilized by native ungulates each winter (elk, mule deer, pronghorn) and may have supported unnaturally high concentrations of elk because of conditioned avoidance behavior from hunting outside the park boundary. A reduction in frequency of natural fires has probably also influenced plant composition, especially on the slope where Douglas-fir increased.

PRIOR USE:

Original is a copy of YNP museum collections # 298. View was plate 90 in Houston, 1976; plate 46 in Houston, 1982; plate 2 in Yellowstone and the Biology of Time.

A3. Description of historical photos of the Gardiner Basin from Yellowstone National Park (Museum Collections).

A4. The Gardiner Basin in 1893, photographer unknown (Museum Collections).



A5. The same location in 1971, documenting a loss of sagebrush in the foreground. Photo taken by D. B. Houston (Museum Collections).

A6. The location photographed again in 1990 by D. B. Houston showing an even greater loss of sagebrush (Museum Collections).

A7. Finally, the same location photographed by the author in 2018 showing almost no sagebrush on the landscape.

A8. The extent of *Alyssum desertorum's* dominance on the landscape. This photo was taken in August 2017.

A9. Evidence of high winds in the Cinnabar exclosure in the Gardiner Basin. This video was recorded in July 2016.

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